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Respiration of potato tubers after injury

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The suggestion for this study of the respiration of injured potato tubers came from some results which were obtained in a previous investigation by the writer (11). In order to obtain sufficient material to make a chemical study of the changes which occurred in the regenerating layer induced by cutting tubers, Mr. N. L. Walbridge, instructor in physics in the University of Vermont, who was assisting the writer on the chemical determinations, and the writer cut in two about thirty tubers and kept them in a cool cellar covered with damp paper. At the end of six days a thin layer (about 1–2 mm. in thickness) was sliced off each cut surface and a similar layer for a check. The tubers were then replaced and allowed to regenerate a new layer, and the slicing operation was repeated in five or six days. Altogether, four such cuttings were made, and the cut slices dried and analyzed separately by Mr. Walbridge. The curious fact came out that the percentage of glucose and of fat increased with each successive cut, while it remained the same in the check samples. It seemed that we had here an example of a summation of stimuli, resulting, each time the stimulus was repeated, in an increased response in the form of a chemical deposit for the healing of the wound. The glucose is used as a source of carbohydrate material for respiration, so the question at once arose:—"Will the respiration show a similar rise with each stimulus?"

Before discussing results obtained, it will be best to call attention to the morphological changes, and to examine some of the literature that has already been published on the subject of respiration in injured plants.

The healing of the cut surface of a potato tuber takes place

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in two phases, provided a fairly warm temperature, dampness, and oxygen are available. A temporary stoppage layer is put in at once during the first day or two, and a new cork cambium regenerates and gives rise to a new skin in the third, fourth and fifth days. The first process consists mostly in the impregnation of the walls of the outer two or three layers of cells with suberin or similar fat-like compounds. These walls are less permeable to water so that the tuber loses less water, and they also exclude bacterial or fungal invaders. The second phase of the healing takes the form of the growth of a new cork cambium and cork layer. A layer of cells, five or six rows deep, free themselves from storage starch, acquire more protein in the nuclei and develop into a cork cambium. The new layer is about eight to ten cells in thickness, and is apparently as efficient in checking transpiration and respiration as the corky covering of the remaining parts of the tuber. The cell walls are suberised and the surface is further protected by three to five layers of cells on the exterior. These cells lose their protein contents and nuclei, but their suberised walls must materially assist in reducing the loss of water and carbon dioxide. The further fact was brought out by the writer that the regenerating layer is filled with glucose, which can be demonstrated micro-chemically with Fehling's solution, the region adjacent to the old skin being especially rich in it. This two-phase healing of wounds in plants has been shown by Priestley and Woffenden (15) to be a common occurrence, not only in the potato, but in a number of other species studied by them.

The physiological aspects of such plant injury have been studied by a number of investigators, by several with reference to the amount of carbon dioxide evolved at various stages in the process, while others have followed the chemical changes induced in injured tubers and bulbs.

Boehm (2) was apparently the first investigator to call attention to the abnormal production of CO_2 in potatoes injured by cutting. He noted that this increase reached its maximum on the second day and then began to drop.

Boehm's later paper (3) laid emphasis on the traumatic effect of the cutting of the tubers on the tissues themselves, regardless of the presence or absence of oxygen. But this theory had already been overthrown by the investigations of

Stich (18) who covered the cut surfaces of the potatoes with neutral gelatin and fastened them together so tightly as to exclude all oxygen, and who found that no evolution of carbon dioxide resulted. The contact of the cut surface with the air was absolutely necessary to induce the reactions which produce the carbon dioxide. Attention should be called to the fact that he washed off the cut surfaces of the tubers with water, before covering them with a 2 mm. layer of 30 per cent gelatin. As will be noted later, this procedure may account partially for the results.

Richards' paper (16) on the respiration of wounded plants is the fullest account that we have of the production of CO_2 after this type of stimulation. Potatoes, carrots, beets, young bean and melon seedlings and various sorts of twigs and leaves were used in the experimentation. The general method was to determine not only the CO_2 produced, but also the oxygen consumed, by means of a modified form of the Pettenkofer apparatus. His data demonstrate that the increased respiration is at its maximum about two days after injury and that the absorbtion of oxygen is in excess of the amount of CO_2 produced. This abnormal use of oxygen and excretion of CO_2 he ascribes to an attempt on the part of the injured plant to free itself from an unnatural condition, that is to say, a cut surface open to the air, and that in the healing process all the vital activities are accelerated. When the open surface is blocked up by new tissue, the protoplasmic process again drops back to normal. Artifically blocking the open wound by applying wet clay would produce the same decrease in the amount of CO_2 formed and oxygen used.

Friedrich's contribution (6) to the study of cut surfaces is on the chemical changes which are induced. Ordinary chemical methods of analysis were used on injured onions, potatoes, apples and quinces. The potatoes that were injured increased in total nitrogen and in acidity, and decreased in carbohydrates. Microchemical tests showed a marked deposit of reducing sugars along the cut surfaces. The reducing sugar is used up in the respiration induced by the healing. The organic acids formed are the intermediate products of respiration, a partial destruction of the glucose into CO_2. The glucose arises according to Friedrich's view from the destruction of the smaller starch grains,

but he gives no evidence of any observations that support this assumption.

Palladin (13) has attempted to distinguish three types of respiration:—(1) the CO_2 has its origin in the nucleic acid; (2) the CO_2 is a product of stimulation; (3) the formation of CO_2 is due to oxidases. The CO_2 produced in injuries would at first be, therefore, of the second type almost entirely, while later it might come partly from the destruction of the nucleic acid. The CO_2 of stimulation is the result of the actual excretion of this gas by the protoplasm itself without the intervention of enzymes or oxidases. Quinine stimulates the protoplasm, as does etherization, and an increase in CO_2 formation is the result.

Kovchoff (9, 10) confirmed on onion bulbs the chemical work of Hettlinger (8) and Zaleski (21), demonstrating the increase in protein in injured tissue, and he discovered further that the greater part of this increase was in the nucleoproteids that are not digestible in pepsin. This accumulation of nitrogenous compounds occurred only in the presence of oxygen, since injured bulbs placed in an atmosphere of hydrogen showed no protein increase. The non-digestible proteins are formed slowly during the first two days, but very rapidly during the following three or four days. Unfortunately his tests did not extend more than six days.

Kovchoff (10) later attempted to demonstrate by comparison of the phosphorus and nitrogen ratios that the formation of these indigestible nucleoproteins was not a form of starvation. The ratio of phosphorus to nitrogen remained the same in injured or uninjured tissue.

Smirnoff's work (17) is interesting in that he determined the amount of intramolecular respiration in injured onion bulbs by placing them in an atmosphere of hydrogen. The respiration which had been measured by Richards, Stich, and others was made up of two components; intramolecular and wound. The latter component only shows in the presence of oxygen, so, when the bulbs were placed in the atmosphere of hydrogen, only the intramolecular respiration remained. Smirnoff shows that this respiration was not increased by the wound stimuli.

The classic paper of Müller-Thurgau (12) on the accumulation of sugar in tubers stored at low temperatures is often

quoted, and may offer some side lights on the problem of respiration and sugar formation in tubers that have been kept at low temperatures. As is well known, potatoes kept at zero Centigrade, or at nearly that temperature, become sweet to the taste from an accumulation of sugar. This investigator concludes from a long series of trials with tubers kept at various low temperatures with a subsequent chemical analysis of them, that the accumulation of sugar is a normal process associated with the rest period of the plants. The enzymes which convert the starch into sugar continue to act even at low temperatures, while respiration is reduced to a minimum. The consequence is an increase in the sugar content. Such sweet tubers, when brought into a warm laboratory, respire more, and germinate quicker, than those kept at higher temperatures. The sugar that has been accumulated is available either for the formation of carbon dioxide, or to feed the young sprouts. The particular contribution that he suggests is that the diastatic enzyme continues to act in the cold, while the respiration hormones, if there are such bodies, are inactive.

Butler (5) more recently has confirmed these conclusions, and has further shown that potato varieties differ in the rapidity with which they accumulate sugar, that the sugar is located mostly at the eyes and apparently very little of it is translocated. He is inclined to associate the accumulation of sugars just at the time sprouts are formed with other metabolic agents.

Votchal's results (20, according to Palladin's Plant Physiollogy) show the presence of a larger percentage of solanin in the injured portions of the potato tuber. Palladin's suggestion that the solanin may serve as a stimulus to respiration is a very plausible one, and may explain also the larger percentage of glucose in the injured portions next to the old uninjured skin, since the solanin is most abundant there and in the neighborhood of the potato eyes. In the ordinary starch layers there is only .002 per cent, while in the skin there is 0.7 per cent (Wehmer, Die Pflanzenstoffe, p. 681). On the other hand, the increase in solanin content may be only another expression of the contact with oxygen, the two processes—increase of solanin and rise of respiration—being coincident, but not dependent the one on the other.

The increased respiration after injury, while it is in part

induced by the healing process, may be regarded as in the main an irritable response of the protoplasm to the stimulus of the contact of tuber cells with the oxygen of the air. These cells, deeply imbedded in the tuber tissue, are under ordinary conditions protected by a cork layer from such a contact, and are only brought to the outer surface by violent means such as the cutting or breaking of the tuber. As Verworn (19) says, "Every living system possesses, as we know, a peculiar and characteristic manner of reacting to stimulation. The muscle responds with a contraction, the salivary cells with production of saliva, the luminous cells with the emission of light." In the cut or injured tuber cells, the response is in the production of carbon dioxide and the deposition of sugar in the injured part. The problems of irritibility have been studied mostly from animal protoplasm. A review of them in their general aspects may be found in the book of Verworn just quoted, especially applicable to the present study being the chapter on "The refractory period and fatigue." The refractory period lies between the successive stimuli. As the organism gradually recovers from a stimulus, it frees itself from the products that have been laid down in the cells as a result. These products may be regarded as the cause of asphyxiation. The presence of oxygen will disintegrate these products and in the course of a varying length of time, the effects of the stimulus and its products will disappear. As long as some of these products remain, the response will not be as great and we say that the cells are in a state of fatigue. Fatigue, therefore, is really only a form of asphyxiation, due to a lack of oxygen supply, or to an insufficient length of time having elapsed since the previous stimulus. If the stimuli come rapidly with very short intervals of rest, fatigue is induced with few stimuli, but if the stimuli come at long intervals, the decomposition products pass off into the surrounding air as carbon dioxide. It has been shown for example that a frog's leg stimulated until completely fatigued will not regain its irritibility in an oxygen free medium, while it will as soon as it is placed in oxygen.

Bose (4), using electrical stimuli on *Mimosa*, found that if he distributed the stimuli so as to allow an interval of rest of fifteen minutes, the responses were all of the same height of curve, but that if only ten minutes intervened there appeared

a fatigue diminution. The objection may be raised to Bose's work that he, by using electrical stimuli, induced various chemical changes, ionizations, etc., in the irritated protoplasm, but it must be admitted that it is probable that that is exactly what occurs as the result of any stimulus, i. e. the response is chemical.

The literature cited above shows that we have accumulated considerable information on the respiration, chemical products, and cell structures involved in injured tubers and bulbs. The present investigation is an attempt to enlarge our knowledge of the effects of repeated cuttings on respiration and reducing sugar content, and of the influence which chemicals and external conditions will bring about in the amount of carbon dioxide produced.

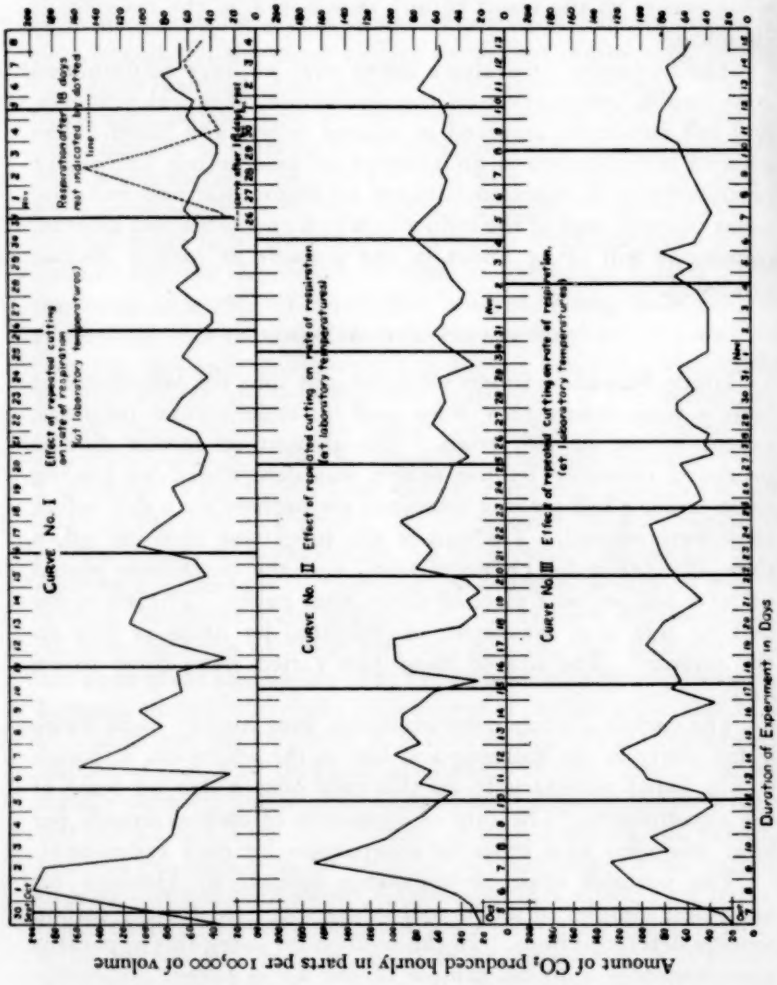
APPARATUS AND METHODS

Green Mountain tubers were brought into the laboratory at least a week before they were used for experimental purposes, except in one or two trials. The amount of carbon dioxide produced normally by the tubers was determined by placing them under a bell jar in a saturated atmosphere for a day before they were injured. The end of the tuber was then cut off, a thin slice taken for chemical tests, and the cut tubers placed under a bell jar on a piece of damp filter paper. The air in the bell jar was kept saturated, as indicated by drops of dew on the interior. The size of these jars varied from three to six liters.

The carbon dioxide determinations were usually made twice a day, early in the morning and late in the afternoon, although it was found necessary to do this only once a day on some of the experiments. The rate of formation of carbon dioxide per hour was used as a basis for comparison for each experiment.

The portable type of apparatus devised by Haldane for analyzing samples of air in coal mines was used for the carbon dioxide determinations. In the method for using this apparatus approximately a 10 cc. sample of the air is taken, accurately measured, the carbon dioxide absorbed by a strong alkaline solution, and the sample re-measured. The difference in the readings is the percentage of carbon dioxide. The most important precaution is to obtain a representative sample. This was

secured by thoroughly stirring the air in the bell jar with a celluloid fan attached to a glass rod, operated from the outside, before the 10 cc. samples were withdrawn. These samples were withdrawn through a pinchcock at the end of a long glass tube


CURVE No. I Effect of repeated cutting on rate of respiration (at laboratory temperatures)
Respiration after 18 days rest indicated by dotted line
CURVE No. II Effect of repeated cutting on rate of respiration (at laboratory temperatures)
CURVE No. III Effect of repeated cutting on rate of respiration. (at laboratory temperatures)
Amount of CO2 produced hourly in parts per 100,000 of volume
Duration of Experiment in Days

extending down into the bell jar to a point just over the cut tubers. The sampling tube of the Haldane apparatus was filled at least three times by passing air contained in the connecting tubes over into the bell jar and filling them with the air from

the bell jar, before the readings were taken. Duplicate readings were taken in nearly all cases, and the two readings usually agreed within a few points. Samples taken at the bottom and at the top of the jar showed no measurable difference in CO_2 percentage after the stirring. The method is accurate to one-tenth of one per cent.

The tubers under the bell jars were kept at laboratory temperature, 21–22° C., but on certain Sundays the temperature fell at times to 16° C. This variation was unfortunate but could not be avoided. In the later experiments, a room which was heated by means of an electrically controlled electric radiator was used. The temperature in this room was maintained at about 23° C., and never sank below 19° C.

The weight of tubers used varied in the various experiments, as did the size of the bell jars. The comparisons were made entirely on the rate of production of carbon dioxide per hour under a given bell jar, with a given lot of potato tubers cut in a certain way.

RESULTS

1. *Effect of repeated cutting on the respiration.* The first set of experiments were conducted to ascertain the effect of repeated cutting on the production of the CO_2 of respiration. Four or five large tubers of a weight approximating 450–500 grams were washed and placed under the bell jar for at least a day before the experiment. The normal rate of respiration of the uninjured tubers having been obtained, the end of the tuber was cut off to a point where the diameter was fairly constant. Usually half stem and half bud ends were cut off to equalize any possible difference in the respiration of the two ends. The cut tubers (not inclusive of the cut-off portions) were replaced under the bell jar, and readings taken again after an interval of 8–12 hours. Two readings a day were usually taken, one early in the morning at between seven and nine o'clock and the second later in the day at from four to six o'clock. This total production of CO_2 was divided by the number of hours to get the rate per hour. The injured tubers were kept under the bell jar for 5–6 days, at the end of which time the respiration had again almost returned to normal. A thin slice, about 1–2 mm. thick, was again cut from each of the tubers and they were replaced under

the bell jar. These operations were repeated every 5–6 days until eight slices had been removed. The data can be best presented in the form of curves, where the height of the curve represents the amount of CO_2 produced per hour in parts per hundred thousand by the injured tubers under one bell jar. CURVES I, II, III, IV, and V present this phase of the study.

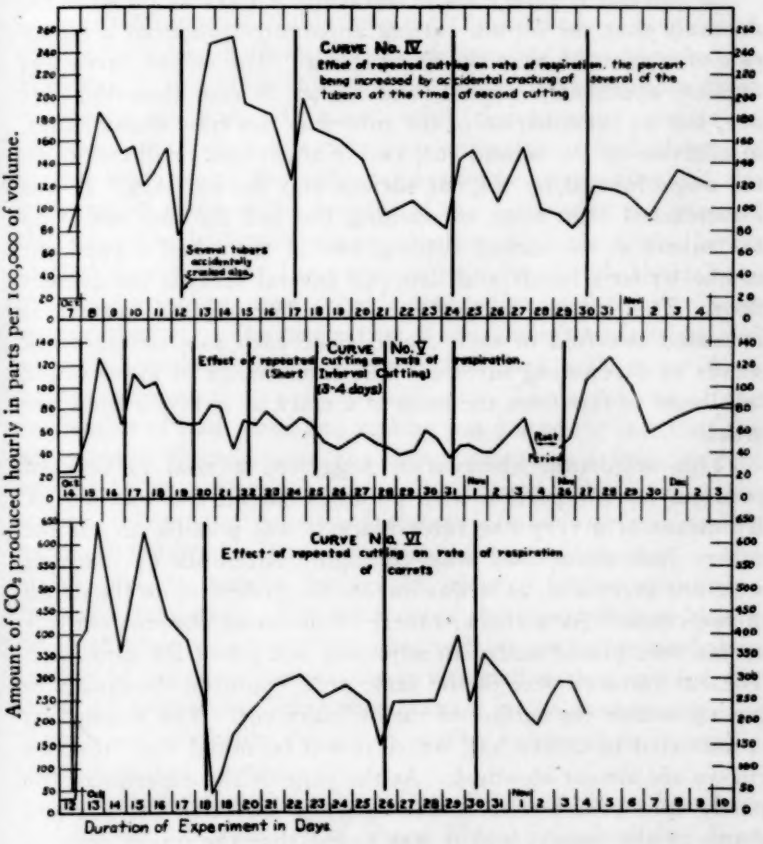
The results of the first cutting are well known from the previous work of Boehm, Stich, Richards, and others, which has been mentioned. The curve of respiration rises after the first day, attains a maximum on the second or third day, and then gradually drops away. The maximum obtained seemed to vary with the various lots of tubers used, and also with their condition. Tubers brought in fresh from the out doors gave a much higher rate of respiration than those which had been kept in the laboratory for a week or two, since the curve of respiration was not only that of injury, but had the added effect, studied by Müller-Thurgau (12), of the rise of temperature induced by the change to the warm laboratory. The difference is illustrated in CURVE I from the respiration of tubers directly from the field, and CURVE II from tubers that had been a week in the laboratory. The second cutting did not produce as high a percentage of respiration in any case, the maximum of the second day being lower in every instance. The general form of the curve, however, was essentially the same.

The third, fourth and succeeding cuttings produced less and less stimulative effect, until the reaction, as indicated in increased CO_2 production, could hardly be noticed at all. The minor fluctuations which occurred between the later cuttings must be attributed to the variations in temperature to which the tubers were subjected in the laboratory. The stimulus of injury to the tubers is to be regarded as one which, if repeated four or five times, fails to produce a response so far as increase of respiration is concerned. Fatigue develops rapidly.

It was thought possible that the stimuli were applied at too long intervals; therefore the tubers whose respiration is recorded on CURVE V, were cut, not every 5–6 days, but every 2–3 days, in the hope of getting a cumulative rise, a stepping up of the reaction. The results, however, showed just the opposite. When the stimuli came at these intervals, the reaction disappeared with only two or three cuttings, and the curve of wound

respiration flattened out with only the irregularities due to variations in the laboratory temperature.

On the other hand, long intervals between the stimuli gave the plant an opportunity to recover from its fatigue, as can be seen in CURVE XIII, where the interval between the cuttings was 10–12 days. The later curves were almost as high as the


CURVE No. IV
Several tubers accidentally cracked also.
CURVE No. V
Rest Period
CURVE No. VI
Effect of repeated cutting on rate of respiration of carrots
Amount of CO2 produced hourly in parts per 100,000 of volume.
Duration of Experiment in Days

first one. The additional 5–6 days seemed to give the tuber a chance to recover its sensitiveness, at least as expressed in respiration, so that when the same stimulus was applied, the response was just about as vigorous as at first. This recovery from fatigue is further illustrated in the latter parts of CURVES I and V. The tubers used in obtaining these curves were kept

in the laboratory, after their susceptibility to injury stimuli had become exhausted, in the case of the first lot for 18 days, and in the case of the fifth lot for 22 days. The results obtained were surprising. The respiration response was almost as good as it had been in the first cutting. The fatigue seemed to have entirely disappeared.

2. *Increase of injury due to cracking.* CURVE IV presents the anomaly that the second cutting apparently produced a higher rate of respiration than the first cutting. The second curve was regular, apparently normal, and higher in rate than the first one, but an examination of the tubers at this time showed that, in addition to the second cut, two of them had small cracks on the angle formed by the cut surface and the old skin. It was remembered then that, in opening the bell jar and removing the tubers at the second cutting, two of them had slipped out of the writer's hands and dropped several feet to the cement floor. The cracks were the result. The injured surface is increased two-fold in each crack, since each side of the crack serves as a respiring surface. The interchange of gases would be almost as fast from the sides of a crack as it would from free areas.

This accidental observation suggested a trial of cracked potatoes for comparison with potatoes cut all the way across. By means of a very fine razor blade it was possible to cut the tubers just about half way through. Attempts at cracking were not successful, as it was impossible to determine the depth of the crack. As a check, tubers of the same size cut entirely across were placed under an adjoining bell jar of the same size. The cut surfaces were of the same area, counting the cracks as having double the surface of the ordinary cut. The respiration is indicated in CURVE XII, where it will be noted that the two curves are almost identical. At the close of the experiment the partly split tubers were broken apart to ascertain the size and depth of the injury, and it was found that the injury covered just half of the cross-section of the tubers.

3. *Respiration after bruising.* The respiration from the cracked tubers was so marked that other common forms of injury were investigated. Bruising was produced by a rubber hammer and by hitting the floor or table with the tubers. As far as possible, breaks in the skin were avoided, although a few

small ones did show after the rather rough treatment to which the tubers were subjected. The tubers were soft in many places. The respiration of the bruised tubers is shown in CURVE XVIII. The slight rise is doubtless due to the broken spots of the skin. The bruising seemed to have little effect provided the skin remained unbroken; contact with the air would seem to be necessary to produce this type of response to the injury stimulus.

4. *Respiration of scabby tubers.* The increase in respiration after infection with *Phytophthora infestans* has been observed by Boehm (3) and other investigators have confirmed this effect of fungus on host. Infection with the parasitic strains of *Actinomyces chromogenus* causes an enlargement and deepening of the lenticels of the tuber and affords an opening for the exchange of gases of the interior of the tuber with the gases of the air. The lenticular tissue, together with the corky layers formed as a result of the parasitic stimulus, is filled with large intercellular spaces that provide an easy channel for the interchange of gases. The respiration of equal weights of scabby and clean tubers kept under adjacent bell jars with moist filter papers is shown in CURVES VII and VIII. The rapid rise of the respiration of both clean and scabby was due to the fact that the tubers were brought into the warm laboratory from a cool storage cellar. After nine days it was noted that one of the scabby tubers had developed storage (*Fusarium*) rot, and it had to be removed. The curve dropped as a consequence. The scabby tubers, weight for weight, showed higher respiration than the clean ones. The presence of the tuber affected by dry rot cast some doubt on the observations so far as scab was concerned, so the experiment was repeated with a new lot, the curve of respiration being shown again to be consistently, although not markedly, higher in scabby tubers than it was in clean ones (CURVE VIII).

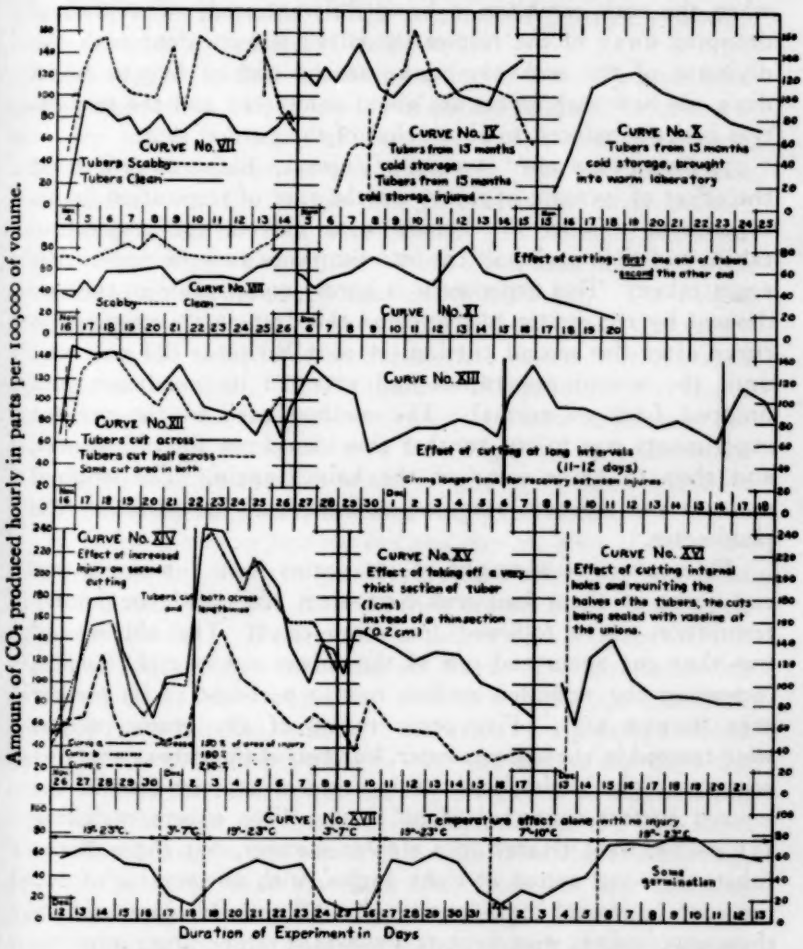
5. *Respiration and recovery from injury of old potatoes from cold storage.* A quantity of Green Mountain tubers had been held in cold storage since the preceding summer—about 15 months. The rate of respiration for such tubers rises rapidly when they are brought into a warm room, as shown in CURVE X, and seems to remain high, at least for some time. This curve only confirms the results of Müller-Thurgau (12) already referred to above.

In order to overcome this rise from a change of temperature, some tubers from storage were kept at laboratory temperature for about a week before being used for the injury experiments (CURVE IX). The respiration was taken for 3–5 days, and after it was found to be fairly constant, the ends were cut off one lot while the others were left as a check. The injured tubers produced the ordinary respiration curve of response, and in almost as marked a degree as those that were fresh from the field or had been harvested a month or two before. The long continued low temperature did not check the response to injury, although it did cause the tubers even when uninjured to maintain a high rate of respiration, the evolution of CO_2 in this case, being, however, a normal process.

6. *The respiration curve in detail.* A careful examination of some of the curves of respiration after injury show two maxima, a high one after the first day and a secondary one after about three or four days, with a pronounced drop between. This comes out in CURVE I after the 2nd, 3rd, 4th and 5th cutting and in the curves formed after the tubers had rested for 18 days, in CURVE II after the 4th, 5th and 6th cutting, in CURVE III after the 1st cutting, in CURVE IV after the 1st and 4th cutting, and in CURVES XV and XVI after both the 1st and 2nd cutting. These respiration data were taken at laboratory temperatures which varied quite a number of degrees so that they could not be depended upon for fine details. In view of the fact that the healing process, as already explained, occurs in two phases, it was deemed advisable to try some injury experiments under more constant temperatures. For this purpose, a room with an electric radiator controlled by a thermostat was employed. The variation here was only between 19–23° C., with the temperature held most of the time at 22–23° C.

A lot of five tubers weighing 930 grams was kept in this room for 5 days and then placed under a bell jar to determine the normal respiration per hour for 24 hours. At the end of this time each of the tubers was cut in two and half placed under each of two six liter bell jars. The curve of respiration is shown in CURVE XIX. Both lots showed a drop after the maximum obtained on the second day, with another rise in the latter part of the third day. After the third day the respiration gradually dropped away during the fourth to seventh days.

A second cutting made on the seventh day gave the peculiar effect of a diminution in the rate of respiration during the day on which the tubers were injured. The second day, the respiration was at its peak, after which a sag appeared in the amount obtained under one of the jars, with a rise again the next day.


Curve No. VII
Tubers Scabby
Tubers Clean
Curve No. IX
Tubers from 13 months cold storage
Tubers from 15 months cold storage, injured
Curve No. X
Tubers from 15 months cold storage, brought into warm laboratory
Curve No. VIII
Scabby
Clean
Effect of cutting- first one end of tubers second the other end
Curve No. XI
Curve No. XII
Tubers cut across
Tubers cut half across
Some cut area in both
Curve No. XIII
Effect of cutting at long intervals (11-12 days)
Giving longer time for recovery between injuries
Curve No. XIV
Effect of increased injury on second cutting
Curve No. XV
Effect of taking off a very thick section of tuber (1cm.) instead of a thin section (0.2 cm.)
Curve No. XVI
Effect of cutting internal holes and reuniting the halves of the tubers, the cuts being sealed with vaseline at the unions.
Curve No. XVII
Temperature effect alone with no injury
Some germination
Amount of CO2 produced hourly in parts per 100,000 of volume.
Duration of Experiment in Days

It is apparent from the above that the shock of injury may check all normal respiration for a time, and that the first recovery phase, during which the cut surfaces are being suberised, produces the first maximum. The second maximum appears

just about as the cell divisions of the new cork cambium are most numerous, i. e. during the third to fourth days. The writer (11) has determined this fact by a series of trials made to secure as numerous cell divisions as possible in this regenerating layer for cytological study. The sag would appear at the time when the cork cambium is being differentiated. The gradual dropping away of the respiration curve is coincident with the divisions of the cork cambium—at the end of five to seven days, the new cork layers are about completed and the respiration is again reduced to about that of the normal skin.

7. *Respiration after increase of injury*. Richards (16) tried the effect of increase of injury on the rate of respiration in his experiment number 6. Tubers were halved, the respiration taken, and then each half cut into six pieces and the respiration again taken. This experiment is hardly comparable to the one devised by the writer to overcome the drop in the respiration curve after the second cutting, in that Richards did not wait until the wound respiration had attained its maximum and dropped back to normal. The method used in the present experiments was to cut another thin slice from the old wound, and then to halve some of the halves again. The original surfaces and the new wounded surfaces were measured by the planimeter.

Five tubers of a weight of 471 grams were cut across one end (part of them bud and part stem end) and the hourly respiration curve followed for seven days. The old wound was then cut again and one of the tubers cut at right angles, increasing the wounded surface to 150 per cent of its former area (CURVE XIV). Five other tubers of 485 grams weight were treated in the same manner, but two of the tubers were cut across at right angles, with an increase of 210 per cent of the injured surface (CURVE *b* of no. XIV). Five tubers, weighing 451 grams, were treated in a similar manner, but three of the tubers were cut across at right angles, with an increase of 210 per cent in wound area (CURVE *c*). All the bell jars used in these experiments were kept at a constant temperature approximating 22–23° C.

The curves of respiration from the second injury rose in all cases markedly higher than those from the original cuts. The amount of increase of injury did not seem to affect the propor-

tionate height, but the response was higher in all cases. It is to be pointed out that this experiment really does not increase the injury on the *old* surface, but opens up new tissues and cells to the action of the oxygen. It is doubtful if the injury stimulus extends more than a few millimeters below the cut; the chemical disturbance (as indicated by the presence of glucose) probably is a very good indication of its limits.

This suggestion that the wound stimulus was very superficial caused the writer to use the lot of tubers followed in CURVE *c* for deep injury. Instead of removing a slice 1–2 mm. thick, a piece 1 cm. in thickness was taken off. The resultant curve showed, however, the fatigue drop in exactly the same manner as when the slices removed were thinner. In the same way some of the tubers from which CURVES *a* and *b* had been obtained were combined, cut deep and replaced under a bell jar. The weight was approximately that of one of the original lots. CURVE XV shows that the reaction is similar to that shown from repeated cuttings of thin slices. The stimulus which produces the wound respiration and the fatigue must extend to some depth into the cell layers. The whole tuber in fact might be in a somewhat stimulated condition and show cell fatigue to repeated irritation. This possibility suggested the following experiment.

8. *Effect of cutting first one end and then the other of the tuber.* Four tubers weighing 380 grams were used after they had been in the laboratory for five days and their normal hourly respiration taken for one day. The ends of the tubers were then cut off, and the hourly respiration taken for six days. This particular lot of tubers did not show as marked a rise due to the injury as have some of the other lots, but there seems to be a great difference in the response among potatoes. At the end of six days the other ends of the tubers were cut off, 282 grams in weight being left, and the new cut surfaces approximating the old ones. The curve of respiration rose higher than from the first cutting. It is to be noted that the respiration from the first stimulus had disappeared before this second cutting. This experiment would indicate that the wound stimulus, while it extends to some depth in the tuber, does not affect all of it, and that, when the tubers were cut across at right angles to the old wound, part of this injury opened up a new surface which had been previously unaffected and was not markedly fatigued.

9. *Effect of internal injury on the rate of respiration.* The work of Bennett and Bartholomew (1) on the respiration of black heart tubers suggested the trial of some tubers cut internally and re-united.

Five large tubers with a weight of 498 grams were cut in two and a cavity about 3 cm. long, 2 cm. wide, and 2 cm. deep was excavated in each half. The amount cut out totalled 23 g. The normal respiration had been taken before injury. The two halves were re-united and bound together with twine, while a layer of vaseline was applied to the place where the cut surfaces came together. This vaseline was renewed several times while the respiration was being taken.

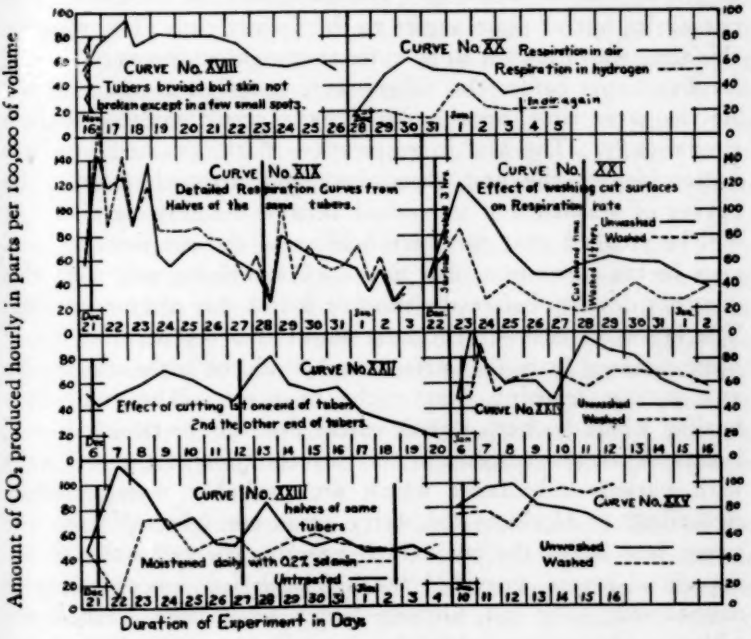
The curve produced (CURVE XVI) was almost exactly the same as that which resulted when the tubers were cut in two, a sharp rise the second and third day, with a gradual dropping back to the normal rate of respiration. The potato skin is apparently quite permeable through the lenticels to the carbon dioxide evolved in the interior cavities. Sections of the tissue lining this internal cavity showed the typical two forms of healing—a darkening of the outermost layer of cells, and a true cork cambium.

10. *Respiration after washing injured parts.* If, as has been suggested by some investigators, the process of respiration is induced by certain bodies known as respiration chromogens, these bodies being present in the plant cells and only becoming activated by the proper conditions, the query rose as to whether these bodies or substances could not be washed out of the surface cells after injury, with a resultant diminishing of the amount of respiration. The answer is in CURVES XXI, XXIV and XXV.

Five tubers weighing 606 grams, which had been in the laboratory a week, were kept under a bell jar for a day to determine the normal respiration. Each tuber was then cut into two equal halves. One lot of the halves was placed at once under a 4 liter bell jar on moist filter paper. The other halves were washed in a vessel in running water for three hours, and were then placed under another similar bell jar.

The respiration curve on the first lot (CURVE XXI) followed the usual course, with a maximum on the second day after injury and a gradual dropping off in the subsequent four or five days. On the other hand, the washed tubers, while they

showed some reaction on one day, dropped at once to the normal and retained this rate. It had been found in the preceding experiments that the loss in the height of the respiration curve could be compensated for by increasing the stimulus (CURVE XIV), the old surface being cut again, and one or more of the tubers cut at right angles. In this way the stimulus could be more than doubled. The first lot were cut only on the old surfaces, but the washed portions were cut not only on the old surface, but each tuber was again cut in two. The first lot


Curve No. XVIII
Tubers bruised but skin not broken except in a few small spots.
Curve No. XX
Respiration in air
Respiration in hydrogen
Curve No. XIX
Detailed Respiration Curves from Halves of the same tubers.
Curve No. XXI
Effect of washing cut surfaces on Respiration rate
Unwashed
Washed
Curve No. XXII
Effect of cutting at one end of tubers, 2nd the other end of tubers.
Curve No. XXIII
halves of same tubers
Moistened daily with 0.2% solanin
Untreated
Curve No. XXV
Amount of CO2 produced hourly in parts per 100,000 of volume
Duration of Experiment in Days

were placed at once under the bell jar while the second lot were washed for an hour and a half before they were replaced under a similar jar. The results with the first lot were a confirmation of the repeated cutting:—a marked lessening in height of the respiration curve, while the washed portion, in spite of the severity of the injury, gave practically no rise in the respiration rate.

This experiment was so interesting that it was thought advisable to try it again under somewhat different conditions.

After securing the normal rate of respiration of a lot of tubers (CURVE XXIV) the tubers were cut into approximately equal halves. One lot of the halves was placed under a bell jar on moistened paper at once, but the other lot was washed (after cutting) for about a half hour before being placed under a similar jar. While the respiration curve of the unwashed portions is higher than that of the washed, it was evident that the results were not nearly as striking as those which had been previously obtained, and the difference lay apparently in the length of time of washing. The same tubers, therefore, were cut again, but at right angles to the former cut. The washing this time was intended to be quite thorough, so it was continued for five hours before the tubers were removed to the bell jar. At the same time, another lot (CURVE XXV) was treated in a similar way. The loss in respiration of the washed lots was noticeable for the first three days, but after that time, the curves of washed and unwashed became roughly parallel. It will be recalled that the later healing of the cut surfaces consists in the formation of a new cork cambium, and that this does not develop before the third or fourth day after wounding. The layers of cells which bring about this regeneration lie at some distance from the surface, and would be little affected by any surface washing that might be given. The temporary healing which is characteristic of the first day or two, however, is superficial, and consists in the impregnation of the cell walls with various substances which are probably water soluble. According to Herklots (7), fatty acids are released from the tissue just below the cut, which suberize the cell walls of the superficial layers, provided the hydrogen ion concentration is maintained. The cut surfaces which have been washed are white in appearance, while the unwashed ones are light gray. Cross-sections made some days later, however, showed that a typical cork layer and cork cambium had been formed under these white and unaltered parenchyma cells on the exterior. This fact would speak against the theory that the formation of cork meristem is dependent on the stoppage of the exterior by an impermeable suberized zone.

The conclusion to be drawn from these experiments is that something is removed from these outer cells which is essential to the increase in respiration. This substance may be the fatty

acids which Herklots postulated, or it may be the respiration activators, or both. The contact of the oxygen of the air with this outermost row of cells is necessary to induce wound respiration, but if this substance or substances are washed out of the cells where it, or they, occur, the deeper placed cell rows are not stimulated, and no large amount of abnormal respiration occurs. The necessity of oxygen in this process is indicated in the following experiment, where the cut tubers were placed in an atmosphere of hydrogen.

11. *Respiration after injury, in an atmosphere of hydrogen.* Five tubers weighing 795 grams were used. They had been in the laboratory about a week. The normal respiration was determined for one day, and then each tuber was cut in two equal parts. One lot was placed under a bell jar with moist filter paper. The other lot was placed under a similar jar and hydrogen passed through for three hours, the air being excluded by a water seal.

The respiration curve was almost flat from the tubers kept in the atmosphere of hydrogen, while it followed the usual course under the bell jar containing air. These results are almost identical with those obtained by Smirnoff (17) from injured onion bulbs. The small amount of carbon dioxide evolved in the atmosphere of hydrogen must be produced anaërobically from the destruction of carbohydrates in the cells. Such a form of respiration is of course independent of the access of oxygen.

12. *Effect of solanin on the wound respiration.* Votchal (20) made the observation that solanin was always formed in unusual amounts in wounded tubers. An experiment was therefore conducted to ascertain the influence that a weak solution of this alkaloid would have on the rate of wound respiration. The normal rate of respiration was obtained for large tubers with a total weight of 860 grams. The tubers were then cut in two and placed under bell jars of the same size, one lot untreated, and the other moistened with a 0.2 per cent suspension of solanin in water. The respiration curve for the two lots of halves is shown in CURVE XXIII. It will be noted that the immediate effect was to check the respiration, but that, later, its effect seemed to be exhausted, and the respiration of the two lots more nearly parallelled each other. The effect was

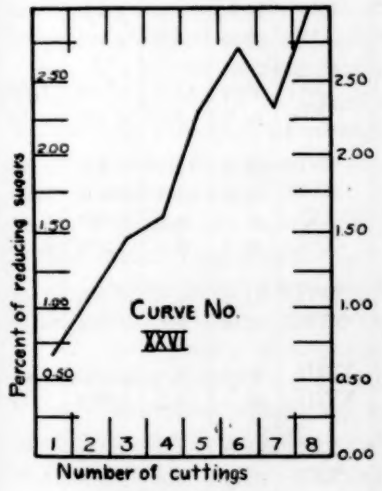
noticeable in the early phase of the healing, when the cells involved were on the surface, but when the deeper placed cork cambium came to be formed, the influence of the solanin, being superficial, could not make itself felt, and the respiration at this later stage was just about the same as on untreated surfaces. A second cutting of the same tubers was made, with similar treatments and in general the same results.

The problem of the effect of the solanin is entirely unsolved. It may be the chemical product which lessens the wound respiration as it increases in concentration, or it may be only one of the accompaniments of the injury to the cells. The fact that it seems to check respiration experimentally would suggest the possibility that, in part, its function is to reduce the respiration rate. No experimental method suggests itself of impregnating the deeper layers of cells with a solanin solution such as would occur if it were produced naturally in a wounded surface. As long, however, as it comes in contact with the actively respiring cells of the outermost layer, it lessens the evolution of carbon dioxide.

13. *Effect of alternating warmth and cold on the height of the respiration curve.* The very irregular curve produced during the periods of repeated cuttings suggested the possibility that, even if a tuber is uninjured, the curve might rise higher than normal after a few days in a very cold room. CURVE XVII presents the respiration during alternating periods of cold and warmth. The tubers were acclimated for about a week in the warm laboratory with electrically controlled temperatures, and then the respiration under a bell jar in a saturated atmosphere was taken for a few days; they were then placed in a very cool room for several days, the respiration being taken every day, before being returned to the warm controlled temperature room. This alternation was repeated several times, as the curve shows. The height of the respiration curve in the warm room, however, did not change much after such treatments, until just at the last rise, when several of the tubers began to sprout, and the experiment was discontinued. The results would seem to indicate that the storage of reducing sugars which Müller-Thurgau (12) found in tubers kept for some time at low temperatures did not occur in sufficient amounts to affect respiration, if the cold storage period was a very short one and the temperatures did not approach zero Centigrade.

EXAMINATION OF THE INJURED TUBERS FOR REDUCING SUGARS

Since the inception of this investigation was due to the accidental discovery that the percentage of glucose increased in the injured portions of potato tubers, expecially if the injury was repeated, the removed slices of the tubers used in the present investigation were dried and analyzed for glucose. If the slices removed happened to be a little thick, the per cent of glucose would drop, since it is nearly all in solution in the outer layers. On the other hand, very thin slices might barely remove all the glucose-containing layer, but none of the underlying tissue, and the apparent percentage would rise. The size of the samples varied, but after they were dried they were usually so small that there was no opportunity for running duplicate determinations. The figures that are given are derived from a single analysis, usually of all the material that was available. The methods recommended as official by the Association of Agricultural Chemists were carefully followed, but, as will be seen, the small amount of material and the variability of that material gave results that were very widely divergent. The analyses are shown in TABLE I.



Very little comment can be made on the results as shown in percentages of glucose. In general, there is a rise in reducing sugars as a result of the injuries, Nos. II and III having a fairly regular increment after each cutting. By combining and averaging the results from the various cuttings, some of the deviations are smoothed out and a fairly regular curve can be obtained (CURVE XXVI).

The glucose (reducing sugars) represents material that can be easily worked over by the regenerating layer to form cellulose, or for oxidizing in the life processes, and it is evident that the plant supplies it in abundance when injured. If the injury is

TABLE 1

Showing in grams, green weight of portions removed, the dry weight, the weight analyzed, and the percentage of reducing sugar found

No. of sample	Green weight	Dry weight	Weight used	Percent reducing sugars	No. of sample	Green weight	Dry weight	Weight used	Percent reducing sugars
I_1	31.5	*	7.322	.35	IV_5	18.5	4.0	3.849	2.23
I_2	15.5	2.3	2.890	.67	IV_6	21.8	7.7	3.318	5.07
I_3	21.2	3.8	3.769	.58					
I_4	22.0	3.8	3.760	1.18	V_1	35.0	6.5	4.704	.07
I_5	28.5	5.3	5.550	2.04	V_2	—	4.0	3.558	.43
I_6	27.5	5.5	5.450	1.96	V_3	21.5	3.7	3.761	1.53
I_7	21.7	4.5	4.026	1.04	V_4	18.0	3.1	3.083	.41
I_8	21.5	5.0	4.134	1.28	V_5	14.5	2.2	2.517	2.84
I_9	33.7	11.7	3.875	1.00	V_6	18.5	3.5	3.186	.56
					V_7	19.2	3.7	3.292	2.55
II_1	—	*	5.722	.49					
II_2	23.8	5.3	5.141	1.74	XIV_1	41.0	12.0	4.994	1.43
II_3	24.5	5.5	5.050	2.47	XIV_2	18.5	6.0	2.761	3.00
II_4	18.5	3.7	3.911	2.30	XIV_3	28.0	6.0	5.132	4.00
II_5	22.7	4.7	4.778	2.08	XIV_4	31.0	6.6	4.111	1.76
II_6	25.0	5.7	5.280	2.22					
II_7	25.5	*	5.421	3.48	XV_1	36.0	11.0	5.002	1.67
II_8	22.5	5.0	4.745	3.06	XV_2	24.0	5.5	4.930	3.13
III_1	31.5	*	5.722	.41	XVI†	73.0	17.0	7.496	1.26
III_2	17.7	6.5	5.977	1.47	XVI‡	63.0	13.5	6.424	2.99
III_3	17.0	3.5	2.788	1.71	XVI_1	31.0	9.3	5.732	2.44
III_4	17.5	3.0	3.134	1.96	XVI_2	26.5	6.0	5.160	4.09
III_5	19.7	2.5	2.802	2.50					
III_6	16.0	3.4	3.188	3.91	$XVII_1$	34.2	10.0	6.193	1.52
III_7	20.0	4.3	3.607	2.44	$XVII_2$	27.0	6.0	2.809	4.36
III_8	21.2	4.0	3.893	4.68					
					$XVIII_1$	21.0	6.0	4.383	1.41
IV_1	18.0	3.4	3.563	2.02	$XVIII_2$	26.0	6.3	3.815	1.23
IV_2	Lost	—	—	—					
IV_3	26.5	5.5	5.312	1.14	XIX	23.0	4.4	3.604	1.77
IV_4	24.5	5.4	5.182	2.19	XIX_1	29.5	6.9	3.938	2.60

* All used.
† Check.
‡ Cut surface.

repeated, the amount of sugar present is increased, although the respiration may fall away. The two processes, while coincident, are not necessarily proportional. The glucose is available for respiration if material is needed, but the plant accomodates itself to repeated injury or becomes fatigued, and less and less goes into the waste form of wound carbon dioxide.

SUMMARY

1. Cutting a potato tuber causes a rapid rise in the rate of respiration during the second and third days after the injury, with a subsequent gradual fall in the curve until the normal rate of the uninjured tubers is attained. If the cutting is repeated in 5–7 days the curve does not rise as high. Repeated cuttings lower the curves until finally the tuber will not respond.

2. Shortening the interval between cuttings to 3–4 days will not step up the effect, the injury stimulus disappears even more quickly.

3. Lengthening the interval between injuries to 11–12 days gave the plant an opportunity to recover, and the curves obtained by the respiration following the later cuttings more nearly approached that attained after the first cutting.

4. If the cut surface remains uninjured for a considerable length of time (18–22 days) the tuber regains its ability to respond to this type of stimuli.

5. A crack in a tuber causes a response almost as large as a cut of twice the area.

6. Bruising the tuber will not induce any marked increase in the rate of respiration.

7. Tubers infected with the scab or rot organisms give a much higher rate of respiration than clean ones.

8. The capacity of response to injury is not lost in very old tubers from storage (15 months).

9. The respiration curve, when examined in detail, shows a maximum the second day while the temporary stoppage layer is in deposition in the outer layer of cells. This first maximum may be followed by a drop in the curve, followed by a second maximum the third or fourth day while the cells of the new cork cambium are dividing. The curve drops away as the new cork layer is completed. Occasionally, after injury, the respiration may drop for twelve hours before rising to the first maximum.

10. The loss in the respiration curves resulting from the later cutting could be easily compensated by increasing the cut surface to 150, 180, 210 per cent of the original area by not only renewing the original injury but adding to it by cutting one or more of the pieces in two. The respiration curve rose even higher than the original one.

11. Deep cutting (removal of a layer 1 cm. thick) did not produce a respiration curve equal to the original one. The injury fatigue apparently extends through a considerable portion of the tuber. Cutting the other end of the tubers produced a curve as high as at first, indicating that the fatigue did not include all the tuber.

12. A cavity on the inside of the tuber produced a marked rise in the respiration, and seemed to have practically the same effect as an external wound.

13. A large part of the effect of the injury on respiration can be removed by washing the cut surface in running water for 1–3 hours. The respiration activators, or the substances on which they act, seem to be water soluble, and to be located mostly in the external cells.

14. The injured tubers respire intramolecularly in an atmosphere of hydrogen, but this respiration is small in amount and does not respond to the injury stimulus.

15. Chemical analyses of the slices cut from the tubers at various times showed an increase in the reducing sugar content. The gradual lowering of the rate of respiration after wounding is coincident with the rise in sugars. The two processes, therefore, do not seem to be dependent on each other.

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Studies of West Indian plants—XIII

Nathaniel Lord Britton

74. UNDESCRIBED SPECIES FROM CUBA

Andropogon virginicus graciliformis Léon, var. nov.

Lower sheaths not equitant, rather terete, glabrous; culms slender and cylindrical from the base, usually producing one or two flowering branches, only from the two or three upper nodes; nodes of the inflorescence long pilose; blades at first narrowly involute or conduplicate from base to apex, becoming flat and flexuous in age, only about 1.5 mm. wide, devoid of long hairs towards the base; spathes becoming reddish, the upper ones 6 to 9 cm. long, much longer than the racemes.

Gravelly soil, Sabana de Motembo, Santa Clara, Cuba (*Léon and Loustalot 11343*). This variety may be readily recognized by its basal sheaths not strongly compressed and equitant as those of typical *Andropogon virginicus* and in its long and very slender stems and narrow leaves. The type specimen is preserved in the herbarium of Colegio de la Salle, Vedado, Havana. We are indebted to Prof. A. S. Hitchcock and Mrs. Agnes Chase for suggestions and help.

Paspalum motembense Léon, sp. nov.

Perennial, glabrous, with a rhizome; culm erect or nearly so, glabrous, about 60 cm. high, simple, the nodes glabrous; sheaths much longer than the internodes, glabrous, striate, compressed, the basal ones overlapping; ligule a delicate membrane 1-1.5 mm. long; blades 20 to 30 cm. long, up to 5 mm. wide, glabrous on both surfaces, scaberulous on the border, conduplicate, acuminate at the convolute apex; panicle short exerted, 15 cm. long, the rachis angled; racemes several, ascending, 2 to 5 cm. long, erect or falcate, their rachis about 1 mm. wide, glabrous, scaberulous on the border; spikelets in pairs, elliptic, 2.5 mm. long, 1.2 to 1.4 mm. wide, the pedicels scaberulous, one of them 1 mm. long, the other two-thirds as long; glumes covering the fruit, thin, glabrous, brownish-yellow; second glume 5-nerved, short pointed; sterile lemma faintly 3-nerved, fruit brown, slightly rugose, shining.

Grassy place, Sabana de Motembo, Santa Clara, Cuba (*Léon and Loustalot 9354*). Related to the South American *P. hydrophyllum* Henr., a much more robust plant, and to the Cuban *P. Wrightii;* this is taller and stiffer than *P. motembense*, from

which it differs also in its aquatic habit and wrinkled spikelets. The type specimen is preserved in the Herbarium of the New York Botanical Garden.

Aristida Pradana Léon, sp. nov.

Perennial, culms cespitose, 60 to 80 cm. long, erect, wiry, somewhat flattened, simple and naked, the upper leaves of the culms, if any, reduced to the elongate, strongly adherent and mostly bladeless sheath; ligule a short ciliate membrane less than 0.5 mm. long; blades firm, closely involute from the base, with usually a few hairs on each side of it, scaberulous on the upper surface, glabrous beneath, flexuous, often splitting, up to 60 cm. long or more; panicle 25 to 35 cm. long, the branches few flowered, usually with one branchlet at base, at first stiffly erect, finally divergent or spreading, the lower ones distant, up to 8 cm. long, the axis and branches scabrous; glumes unequal, 10 to 12 mm. long, the first caducous, scabrous on the keel, 1-nerved, awn-tipped, the second glabrous, awn-tipped from a bifid apex; lemma 15 to 17 mm. long, including the short pilose callus about 1 mm. long, and the dark colored scaberulous beak; awns unequal, ascending, the central one slightly recurved, 2 to 3 cm. long, the lateral ones somewhat approximate, one-half as long as the central one or little more.

Arid rocky silicious hillside, Peladeros de Jauco, southwest of Baracoa, Oriente, Cuba (*Léon 12299*).

This species is allied to *A. divaricata* Humb. & Bonpl. of Mexico, but may be distinguished by its much longer and closely involute leaves. It is named in honor of Sr. Enrique Prada of Jauco, who helped very efficiently in collecting work. The type specimen is preserved in Colegio de la Salle Herbarium, Vedado, Havana.

Chloris Morales-Coelloi Léon, sp. nov.

Perennial, glaucous; culms cespitose, erect, glabrous, compressed, freely branching from the lower nodes, 50 to 80 cm. tall; sheaths keeled, often longer than the internodes, glabrous, the basal ones overlapping; ligule a short ciliate membrane about 0.5 mm. long, with a few hairs behind on each side; blades flat or conduplicate, glabrous on both surfaces, abruptly pointed at apex, 8 to 20 cm. long, 2 to 4 mm. wide; inflorescence finally long exserted; spikes 5 to 11, mostly 6 or 7, ascending, finally divergent or spreading, straight or recurved, sometimes flexuous, 6 to 9 cm. long; axis of inflorescence 1 cm. long or less, the rachis of the spikes scabrous and densely pubescent at base; spikelets, exclusive of the awns, mostly 3 to 3.4 mm. long, appressed, im-

bricate; glumes unequal, acuminate or awn-tipped, scaberulous on the nerve, the second 3 mm. long, the first more than one-half as long; fertile lemma pale, five times as long as wide, wider in the middle, 3-nerved, villous on the callus, short villous on the marginal nerves from base to apex, and often on the keel, from above the base to the middle, the awn 8 to 12 mm. long; sterile lemma 1 to 2.2 mm. long, wider below the apex than at base, acute at apex, its awn 6 to 10 mm. long; some of the lower spikelets include sometimes a second awned sterile floret.

In sandy ground, at Cajobabo, not far from the mouth of Jojó River, Oriente, Cuba (*Léon 12320*). Named in honor of Colonel Morales Coello of the Cuban Navy, in recognition of his effective help. This species is of *Chloris Sagraeana* relationship, but a much taller plant; it also differs in its longer and broader leaves and more leafy stems. The type specimen is preserved in Colegio de la Salle Herbarium, Vedado, Havana.

Peperomia Roigana Trelease, sp. nov.

A puberulent suberect fleshy herb; stem slender (2 mm.); leaves in crowded whorls above, more separated below, about 4 at a node, somewhat angularly suborbicular or slightly ovate or obovate, obtuse, sessile, rather small (10 × 12–14 × 15 mm.), drying opaque, obscurely 3-nerved by transmitted light and finely pellucid-punctulate; inflorescence unknown.

Mogote de la Bandera, Sierra de Viñales, Pinar del Rio, Cuba, (*Roig & Azcuy 2902*).

Torrubia Leonis Standley, sp. nov.

Shrub 2 m. high, the branches grayish, the branchlets densely brownish-tomentose or in age merely puberulent, evenly leafy, with short internodes; petioles slender, 6–15 mm. long, brownish-tomentose; leaf blades oblong-elliptic or narrowly elliptic, 4–7 cm. long, 1.7–3.3 cm. wide, rounded or very obtuse at apex, obtuse or rounded at base or sometimes acute, subcoriaceous, above deep green, lustrous, with obsolete venation, densely short-villous when young but in age only sparsely short-villous or glabrate, beneath slightly paler, copiously villous even in age with short slender spreading hairs, the lateral nerves very slender and irregular; pistillate peduncles slender, 1–2 cm. long, thinly brownish-tomentose, the inflorescence cymose, few or many-flowered, the flowers sessile; pistillate perianth tubular, 1.5–2 mm. long, with spreading limb, glabrous or nearly so; style exserted.

Type in the herbarium of the New York Botanical Garden, collected on limestone rocks at the top of the Sierra de Anafe, Province of Havana, Cuba, May 6, 1924. (*Brother Léon 11622.*)

There are only a few species of *Torrubia* that have pubescent foliage. The present plant is related to *T. cuspidata*, of Grenada and Trinidad, but differs conspicuously in leaf characters.

Tounatea cubensis Britton & Wilson, sp. nov.

A small tree, the young twigs, petioles, and rachis more or less densely pubescent with dark brown hairs. Leaves odd-pinnate, 1.5–2.6 dm. long, the leaflets 13 or 15, elliptic-lanceolate to elliptic-oblanceolate, 5–9.5 cm. long, 2–3 cm. broad, short-petioled, the base obtuse, the apex acuminate, finely reticulate-veined on both surfaces; pod ellipsoid, about 4.6 cm. long.

Valley of the San Juan, Pinar del Rio, Cuba (*J. T. Roig 3162*, April 5, 1924, foliage, type; fruit sent by Dr. Roig from Pinar del Rio, June 1925). This is the first record of the genus *Tounatea* in Cuba. In leaf form it approaches *Tounatea caribaea* (Griseb.) Taub. of the Lesser Antilles.

Bunchosia linearifolia P. Wilson, sp. nov.

Shrub about 3 m. tall, with grayish branches. Leaves linear or somewhat linear-obovate, 3–6 cm. long, 2.5–5 mm. wide, rounded at the apex, acute at the base, lustrous above, dull and faintly nerved beneath, the petioles 2–3 mm. long; drupes subglobose, 10–12 mm. in diameter, apiculate.

Type collected in thickets between Jauco and Cajobabo, Oriente, Cuba (*Brother Léon 12062*). Related to *Bunchosia Leonis* Britton & Wilson, of Cuba, but differing in its linear-obovate leaves.

Byrsonima motembensis Britton & Small, sp. nov.

A shrub 2 m. tall or less, with warty-rugose gray bark and red-strigillose twigs. Leaves mainly on the twigs, early deciduous from the branches, the blades cuneate to obovate-cuneate, 2–6 cm. long, obtuse or abruptly short-pointed, grayish-green, somewhat lustrous and with minute scattered hairs above, paler, dull, somewhat reticulate, and with minute scattered hairs beneath, at least during anthesis, short-petioled, the petioles hairy like the twigs when young; panicles raceme-like, peduncled, rather few-flowered, the peduncle and pedicels pubescent like the twigs, but the hairs often early deciduous from the peduncle; bracts shorter than the pedicels, lanceolate; sepals ovate to orbicular-ovate, 3–3.5 mm. long, obtuse, red-pubescent, corolla 12–15 mm. wide; petals 7–9 mm. long, with orbicular-reniform claws, the blade of one smaller and the claw stouter than in the others; filaments clavate, 2–2.5 mm. long; anthers fully

2 mm. long, blunt or notched at the apex, acute at the base; styles subulate, curved at the apex; fruits not seen.

In thickets of Sabana de Motembo, Santa Clara, Cuba, August 28, 1922 (*Brother Léon and A. Loustalot 11370*).

Leucocroton pallidus Britton & Wilson, sp. nov.

A scurfy-pubescent shrub with slender light brown twigs. Leaves coriaceous, oblong-linear, 5–12 cm. long, 5–10 mm. wide, pale green above, grayish green beneath, mucronate at the apex, obtuse or acute at the base, short-petioled, the midvein impressed above, prominent beneath, the lateral veins rather prominent on both sides, diverging at right angles to the midvein; flowers and fruit unknown.

Forest on Mesa de Prada, Oriente, Cuba (*Brother Léon 11960*). Similar to *Leucocroton saxicola* Britton, but with longer and narrower leaves.

Pachyanthus Lunana Britton & Wilson, sp. nov.

A shrub with ferruginous twigs. Leaves ovate, 5–5.7 cm. long, 2–3.2 cm. broad, glabrous above, pubescent beneath with mostly scattered stellate ferruginous hairs, acute at the apex, subcordate at the base, coriaceous, petioled, 5-nerved, the veins and lateral nerves prominent beneath, slightly impressed above; inflorescence short peduncled; calyx about 4 mm. long, 4 mm. broad, pubescent with shaggy hairs, its lobes oblong, 2 mm. long.

Lomas de Banao, Santa Clara, Cuba (*Antonio Luna 8*). Related to *Pachyanthus Clementis* P. Wilson, of Cuba, from which it differs in its short-ovate leaves.

Icacorea baracoensis Britton & Wilson, sp. nov.

A small tree 5–6 m. high, the twigs and branches glabrous. Leaves oblanceolate, 5–11 cm. long, 1.8–4 cm. broad, obtuse at the apex, cuneate at the base, indistinctly veined, glabrous, the margin entire, short-petioled; branches of the inflorescence corymbiform, the lower pedicels elongated; sepals 5, triangular, acuminate, 0.9 mm. long, 0.8 mm. broad; petals 5, elliptic-ovate or elliptic, 3 mm. long, 2 mm. broad, obtuse at the apex.

On rocks, Sierra de Imias, Oriente, Cuba (*Brother Léon 12256*). This plant differs from nearly all of the Cuban species of *Icacorea* in its corymbiform inflorescence.

Bumelia Roigii Britton and Small, sp. nov.

Tree with gray branches and sparingly pubescent twigs, the shoots sometimes with axillary subulate thorns: leaves persistent;

blades coriaceous, obovate, rhombic-obovate or somewhat cuneate, 3–7 cm. long, rounded at the apex, smooth, glabrous, and shining above, closely tawny-pubescent beneath when young with the hairs fading or deciduous in age, acuminate at the base, short-petioled: flowers not seen: fruit large, apparently about 1.5 in diameter.

Between Cape San Antonio and Morro de Piedras, Pinar del Rio, Cuba, April 13, 1924, (*Roig 3256*, type, and *3257*.)

The specimens indicate, by the leaves, a relationship between this species and *Bumelia loranthifolia;* the fruit of *B. Roigii*, however, is much larger than any heretofore found in the former species.

Maba Leonis Britton & Wilson, sp. nov.

A shrub with grayish brown strigose-pubescent twigs. Leaves elliptic to oval, occasionally somewhat ovate, 1.5–3.5 cm. long, 0.8–2.2 cm. broad, spinulose-apiculate at the apex, rounded or obtuse at the base, finely reticulate veined on both surfaces, pubescent beneath with appressed hairs or glabrous; petioles 2–2.5 mm. long; young fruiting calyx lobes suborbicular, 6–7 mm. broad, densely strigose pubescent on the back; ovary strigose-pubescent.

Thickets near Cojimar, Havana, Cuba (*Brother Léon 6269*, type; *5609*). Related to *Maba Grisebachii* Hiern, of Cuba, from which it differs in its elliptic or oval leaves which are finely reticulate-veined.

Neobracea angustifolia Britton, sp. nov.

A shrub or small tree, with slender branches, the leafy twigs densely short-pilose. Leaves linear-oblong, subchartaceous, 4–7 cm. long, 8–10 mm. wide, densely tomentose, the venation rather prominent beneath, the apex obtuse, the base narrowed, the petioles 2–3 mm. long; inflorescence few-flowered, peduncled, shorter than the leaves, pilose; calyx-segments lanceolate, acuminate, pilose, about 3 mm. long; corolla purplish, about 1 cm. long.

Rocky soil between Santa Cruz and Los Coyuelos, Pinar del Rio, Cuba (*Roig 3227*). In general appearance this plant is similar to *Neobracea bahamensis* Britton, of Cuba and the Bahamas, but differs in its much smaller corolla and narrower leaves.

Tournefortia Roigii Britton, sp. nov.

Shrubby, the twigs and inflorescence sparingly pubescent with short white appressed hairs. Leaves oblong to oblong-

elliptic, 4–7 cm. long, dark green above, pale green beneath, sparingly pubescent with short white hairs on both sides, the venation prominent beneath, the apex acuminate, the base cuneate, the petioles short; branches of the slender-peduncled cymes many-flowered, 6-9 cm. long; sepals linear-lanceolate, acuminate, 3 mm. long; corolla-tube nearly glabrous, 4 mm. long, its lobes ovate, about 1 mm. long; anthers ovoid, 1 mm. long; berries globose, about 6 mm. in diameter.

Open places, El Gato, Pinar del Rio, Cuba (*Roig 3208*). Related to *Tournefortia bicolor* Sw., of the West Indies and continental tropical America, but differing in the prominent venation of its lower leaf surface.

Tournefortia Leonis Britton & Wilson, sp. nov.

A vine 3 m. or more long, the young twigs densely pubescent with appressed brownish hairs. Leaves narrowly oblong or oblong-elliptic, 2–4.3 cm. long, 4–10 mm. wide, acute at the apex, nearly glabrous above or with short scattered appressed hairs on both sides, the petioles 2–3 mm. long; cymes short-peduncled; calyx about 1 mm. long, appressed-pubescent, its narrowly lanceolate lobes acute; corolla-tube 2 mm. long, the linear lobes 2.5 mm. long; fruit depressed, about 4 mm. broad, glabrous.

Type from coastal thickets, Jauco Abajo, Oriente, Cuba (*Brother Léon 12383*); also collected between Sabana and Maisi (*Shafer 7910*). Related to *Tournefortia volubilis* L., from which it may be distinguished by its much narrower leaves.

Callicarpa Roigii Britton, sp. nov.

A shrub, the stout branches, petioles, inflorescence and lower leaf-surfaces densely grayish-floccose, becoming glabrate when old. Leaves broadly ovate, submembranous, 6–10 cm. long, strongly pinnately veined, serrulate, the apex acute or acuminate, the base obtuse or rounded, the stout petioles 8–15 mm. long; cymes stout-peduncled, densely many-flowered, shorter than the leaves, 4–7 cm. broad; pedicels very short; calyx campanulate, subtruncate, 1 mm. long; corolla white, about 3 mm. broad, its lobes rounded; fruit apparently black, about 4 mm. in diameter.

Rocky places, Bolondron, Pinar del Rio, Cuba (*Roig 3220* type, in flower April, 1924); Punta de la Jaulu (*C. Wright 3169*, in fruit, Dec. 22). Referred by Grisebach to *C. acuminata* Kunth. Related to *Callicarpa acuminata* H.B.K. of Mexico and Central America.

Solanum lomensis Britton & Wilson, sp. nov.

A tree 6–8 m. high, the twigs and branches armed with brownish prickles 2–4 mm. long, densely hispid with ferruginous, long-stalked, stellate hairs. Leaves broadly elliptic, 7–14 cm. long, 4.5–8.5 cm. broad, acute to short-acuminate at the apex, rounded at the base, coarsely sinuate undulate, rather dull and with few slender prickles above, the midvein and primary veins impressed, densely hispid beneath with stalked stellate hairs, the midvein and primary veins often rather prominent; petioles 7–15 mm. long; inflorescence 5–10 cm. long; calyx about 2 cm. in diameter; corolla 3.8 cm. in diameter; anthers 6–6.5 mm. long, attenuate at the apex.

Loma San Juan near Loma del Gato, Oriente, Cuba (*Brother Léon 2520*, type; *12353*). Similar to *Solanum Gundlachii* Urban, of Cuba, but differing in its indumentum.

Rondeletia myrtacea Standley, sp. nov.

Shrub 3–4 m. high, the branches terete, reddish brown or grayish, with short or elongate internodes, glabrous or when young sparsely puberulent; stipules broadly triangular, 1.5–2 mm. long, subulate-acuminate, sparsely short-pilose near the apex; leaves opposite, the petioles 2–10 mm. long, glabrous; leaf-blades very variable, ovate-elliptic to oval or oblong-elliptic, 2–6.5 cm. long, 1–3 cm. wide, rounded or obtuse at apex, rounded to cuneate at base, coriaceous, glabrous, lustrous above, the venation prominulous, beneath dull, the costa slender, salient, the lateral nerves about 6 on each side, straight, arcuately anastomosing remote from the more or less revolute margin; inflorescences terminal, few or many-flowered, 3–6 cm. long, cymose-paniculate, the pedicels slender, mostly 3–10 mm. long, glabrous or with a few minute appressed hairs; lower bracts leaf-like, 3–7 mm. long, elliptic or broadly ovate, the upper linear or lance-subulate; bractlets subulate, 1–1.5 mm. long; hypanthium glabrous or with a few minute appressed hairs; calyx-lobes 5, 1.5–2 mm. long, oblong-spatulate, contracted below, rounded or obtuse at apex; corolla-tube 5–6 mm. long, ampliate above, pilose with minute whitish erect-patent hairs, the 5 lobes orbicular, 2–2.5 mm. long; capsule subglobose, 3–5 mm. long, glabrous or glabrate; seeds 1–1.5 mm. long, compressed, yellow-brown, coarsely reticulate, attenuate at each end.

Type in the herbarium of the New York Botanical Garden, collected in gravelly soil near Jauco, Mesa de Prada, southern Baracoa region, Cuba, July 17 to August 4, 1924 (*Brother Léon 11966*). The following collections, from the same region, also belong here: Mesa de Prada, *Léon 11946;* Jauco Arriba, *Léon 12016.*

In general appearance this is very similar to *R. Ekmanii* Britton & Standley, but that species differs in having narrow calyx-lobes which are broadest at base.

Rondeletia ingrata Standley, sp. nov.

Shrub 4 m. high or less, the branches stout, terete, blackish or gray, the branchlets densely pilose with short ascending hairs, the internodes 2–4 mm. long; stipules triangular or broadly triangular, 1.5–2 mm. long, acute, erect, sericeous; leaves opposite, the petioles stout, 1.5–3 mm. long, minutely grayish-pilose; leaf-blades oblong-elliptic, 6–15 mm. long, 3–7 mm. wide, obtuse or rounded-obtuse at apex, obtuse at base, thick-coriaceous, with revolute or subrevolute, much thickened margins, green above, the venation obsolete, when young densely pilose with minute appressed hairs, in age glabrate, beneath covered with a very dense, minute, grayish tomentum, along the nerves sericeous with longer hairs, the costa and lateral nerves elevated, the veins prominently reticulate; inflorescences axillary, usually 3-flowered, sometimes 1-flowered, the peduncles stout, 2–3 mm. long, the flowers sessile; bracts and bractlets deltoid; hypanthium densely tomentose; calyx-lobes usually 5, sometimes 4, oblong-ovate, obtuse, 1.5 mm. long; corolla not seen; capsule globose, 3 mm. in diameter, densely tomentose; seeds minute, compressed, brown, exalate.

Type in the herbarium of the New York Botanical Garden, collected on dry gravelly hills, at Cajobabo, valley of the Río Jojó, southern Baracoa region, Cuba, July 17 to August 4, 1924, (*Brother Léon 12415*). Also collected in the same region, at Jauco Arriba (*Brother Léon 11865*).

Related to *R. camarioca* Wright and, according to description, to *R. Norlindii* Urban. The former differs in the velvety pubescence of the upper leaf surface; the latter in its 1-flowered peduncles and smaller leaves, glabrous on the upper surface.

Rondeletia gaultherioides Standley, sp. nov.

Shrub, the stout branches terete, dark red-brown, with elongate internodes, when young densely pilose with long ochraceous erect-patent hairs; stipules lance-ovate, 5–8 mm. long, acuminate, persistent, densely appressed-pilose; leaves opposite, the petioles stout, 3–5 mm. long, pilose with subappressed hairs; leaf-blades ovate-oval to oblong-elliptic, 3–10 cm. long, 1.7–5.5 cm. wide, abruptly acute to obtuse at apex, rounded or shallowly cordate at base, thick-coriaceous, somewhat lustrous above, when young sparsely appressed-pilose but soon glabrate, the costa impressed, the other venation prominulous, beneath dull, sparsely

pilose with slender, closely appressed hairs, more densely pilose along the nerves, the costa salient, the lateral nerves very prominent, 5 or 6 pairs, nearly straight, ascending at an angle of 45°, arcuately anastomosing near the margin; inflorescence terminal, subsessile, 1-flowered, subtended by lanceolate to rhombic-ovate bracts, these longer than the capsule, appressed-pilose; capsule subglobose, 5 mm. long, densely appressed-pilose, the 4 persistent calyx-lobes (imperfect) oblong, 7 mm. long, densely appressed-pilose outside.

Type in the herbarium of the New York Botanical Garden, collected on rocky banks of Arroyo Bayajá, Sierra Maestra, south of Nagua, Oriente, Cuba, August 8, 1922 (*E. L. Ekman 14759*).

The foliage of this plant is suggestive of *R. correifolia* Griseb., but the form of the inflorescence is unlike that of any of the Cuban species of *Rondeletia*.

75. UNDESCRIBED SPECIES FROM TRINIDAD

Gravisia aripensis N. E. Brown, sp. nov.

Leaves 60–75 cm. or more long, 4½–5 cm. broad, broadly strap-shaped, concave; sides parallel up to about 5–6 cm. below the apex, where they incurve to an acute and shortly mucronate point; margins armed with small horizontally spreading pale brown (? green when alive) prickles 1 mm. long and 3–5 mm. apart; surface glabrous, very minutely punctate (not lepidote). Scape 13–14 cm. long in the only specimen seen, 7 mm. thick, clothed with light brown wool and bearing two glabrous sheathing acute bracts 5–7 cm. long, and terminating in a dense subglobose inflorescence 7–8 cm. long and 7–8 cm. in diameter, composed of 4–5 spherical bright pink flower-heads, each about 4 cm. in diameter and sessile in the axil of a large elliptic obtuse mucronate pink outer bract 5–6 cm. long and 4–5 cm. broad. Flowers numerous in each cluster or head. Bracts about 3–3½ cm. long, 10–15 mm. broad, ovate-lanceolate, acute, tipped with a spine 3–4 mm. long, slightly woolly or becoming glabrous. Sepals 15 mm. long, spine-tipped, the lower two-thirds having unequal membranous inrolled margins, one margin about 3 mm. broad and the other 1 mm. broad and more acutely narrowed into the spine than the broad margin, woolly. Petals not seen in perfect condition, but apparently about as long as the sepals and lanceolate. Stamens about three-fourths as long as the petals, absent in two flowers examined; anthers 3½ mm. long, versatile, oblong, with a blunt mucro. Style rather shorter than the stamens; stigma entire.

Trinidad: Heights of Aripo, growing on trees, Jan. 1922 (*Broadway 9917*).

I have placed this very distinct plant under *Gravisia* because in general appearance it seems more nearly allied to *G. aquilega* Mez, than to any other in the Kew Herbarium. But the flowers are not in a sufficiently good state to admit of complete details being given. I could not, however, detect any ligules upon the petals, nor did I find any pollen to examine. The habit of its inflorescence would seem to distinguish it from *Aechmea*. [N. E. Brown.]

Piper maraccasense Trelease, sp. nov.

Flowering internodes brown hirsute-tomentose; leaves subelliptic-oblong, somewhat acuminate, equilaterally rounded or barely subcordulate at base, rather small (3.5–4.5 × 9–11 cm.), pinnately nerved from below about the upper third, the rather prominent nerves 5–7 × 2, glabrous and somewhat glossy above and finally bullate, brown appressed-hairy on the nerves beneath; petiole short (5–scarcely 10 mm.), scarcely winged, densely brown-hairy; spikes opposite the leaves, rather slender and short (scarcely 4 × 40 mm.); peduncle short (5 mm.), brown-subtomentose; bracts concave-inflexed, hairy; flowers sessile, perfect; stigmas 3, sessile, berries subglobose, indented, glabrous.

Maraccas, Trinidad, (Trinidad Bot. Gard. Herb. *2613*, collected in 1845). Type at the New York Botanical Garden).

Coccolobis quadrifida Britton, sp. nov.

A small tree with stout somewhat flexuous, glabrous twigs. Leaves elliptic, coriaceous, strongly reticulate-veined on both sides, glabrous, 7–10 cm. long, shining above, the apex acute, the base obtuse, the stout petiole 1–1.5 cm. long; ocreae membranous, about 12 mm. long or shorter, their lobes acuminate; spikes slender, densely flowered, 6–8 cm. long, numerous, glabrous, occasionally forked at the base, short-peduncled, 6–10 cm. long; flowers sessile; buds about 2 mm. long; sepals 4; stamens 8, white; stigma 2-cleft.

Tocuche, Trinidad (*Trinidad Herbarium 11012*, collected by R. O. Williams April 28, 1925).

Elsota lophosoma Blake, sp. nov.

Branches and branchlets densely and softly pilosulous with antrorse-curved, yellowish or in age fuscescent hairs; leaves oval-ovate or oval-oblong, obtuse, papery, softly incurved-pilosulous on both sides, more densely so beneath; racemes terminal; fruit about 6 cm. long, sordid-pilosulous, the cell subglobulose, about 1 cm. long, each side covered with about 5

elevated anastomosing thick blunt crests (about 2 mm. high), the upper margin of the cell bearing a repand-denticulate wing-margin about 3 mm. high, this truncate or emarginate at base of proper wing and not decurrent on it, the proper wing obliquely obovate, about 5 cm. long, 7 mm. wide at base, 2 cm. wide above the middle.

Shrub, doubtless scandent, branching; petiolar glands slender, peziziform, 0.5 mm. long; leaves distichous; petioles densely yellowish-pilosulous, 1–2 mm. long; leaf blades 2.5–4.5 cm. long, 1.7–2.3 cm. wide, rounded at base, dull brownish-green above, slightly paler beneath, loosely prominulous-reticulate on both sides, the lateral veins 7–10 pairs; racemes terminating leafy branches, solitary, in fruit 4 cm. long or less, pubescent like the stem, the bracts deciduous; flowers unknown; proper wing of fruit curved at apex, repand on lower margin, with numerous subparallel veins.

Trinidad: Road to Maraccas Bay, 10 July 1924, (*R. O. Williams, W. G. Freeman, and E. E. Cheeseman 11246;* type in herbarium of Royal Botanic Gardens, Trinidad and Tobago; photog. and fragm. in U. S. Nat. Herb., and in Herb. N. Y. Bot. Gard.).

A species allied to *Elsota coriacea* (Bonpl.) Blake and to *E. sylvestris* (Schlecht.) Kuntze, and characterized primarily by the numerous thick blunt crests of the fruiting cell. The description of *Securidaca tenuifolia* Chod., of Trinidad, suggests this species, but a fruit received from Berlin of Trinidad Bot. Gard. Herb. no. 2703, described by Chodat as a velvety form of *S. tenuifolia*, proves to be entirely different from the fruit of *E. lophosoma*.

Pedilanthus ierensis Britton, n. sp.

Stem glabrous, tall, erect, up to 2 m. high. Leaves broadly ovate, rather thin, glabrous, the larger ones 8–15 cm. long, 5-10 cm. wide, the venation widely spreading, the apex bluntly acute, the base narrowed, the stout petiole about 1 cm. long or shorter, the midvein not flanged beneath; flowers similar to those of *P. tithymaloides* but smaller.

Penal Rock Road, Trinidad (*Britton, Hazen and Mendelson 1093*). In flower, March 28, 1920.

Metastelma Freemani, N. E. Brown, sp. nov.

Stem about 1 mm. thick, with internodes 10-20 mm. long, terete, puberulous along two opposite rather broad lines with strongly curved very short hairs. Leaves opposite, apparently

slightly deflexed; petiole 1–1½ mm. long, minutely puberulous; blade 9–13 mm. long, 4–8 mm. broad, elliptic or elliptic-oblong, obtusely rounded at both ends or slightly and broadly cuneate at the base, minutely apiculate at the apex, entire, glabrous on both sides. Flowers in small branching or simple axillary racemes 3–10 mm. long, minutely bracteate, and minutely puberulous on the axis, pedicel and calyx. Pedicels ½–1 mm. long. Calyx-lobes 1 mm. long, oblong, rounded at the apex. Corolla 5-lobed; tube 1 mm. long; lobes 1½ mm. long, oblong, subacute, with thickened microscopically puberulous margins within, glabrous on the back. Coronal lobes 5, arising from the sinuses between the corolla-lobes, about 1 mm. long, linear-lanceolate, acute, bent outwards just below the middle and upcurved at the apex. Staminal column 1½ mm. long, arising shortly above the base of the tube of the corolla and exserted from it, much dilated at the truncate apical part. Fruit not seen.

Balandra Bay, Trinidad, (*W. G. Freeman 11310*).

The genus *Metastelma* is one that urgently requires a thorough revision, for as understood by modern authors and as defined in Bentham & Hooker, Genera Plantarum **2**: 755, it comprises three very distinct types of coronal structure, which in other parts of the order are held to constitute generic distinction, and there seems no valid reason why these differences should not be considered of generic value in this case. The three types are: 1, Plants with the coronal lobes inserted at the sinuses of the corolla. 2, Plants with the coronal lobes inserted at the base of the staminal column. 3, Plants with the coronal lobes inserted at the top of the staminal column.

Originally the genus *Metastelma* was founded by Robert Brown upon a plant collected in the Islands of St. Croix and St. Christopher, having the coronal lobes inserted at the sinuses of the corolla (type 1). This plant (*M. parviflorum* R. Br.) I find upon comparison with the type to be identical with *Thompson 499*, collected on St. Croix, and *M. Freemani*, above described, has the same type of structure and undoubtedly is a true species of *Metastelma*. But modern authors seems to have understood type 2 as being the typical structure of *Metastelma*. While K. Schumann in Engler, Pflanzenfamilien **4**[2]: 229 has placed plants having the typical structure of *Metastelma* (i. e. type 1) under the genus *Irmischia*, founded by Schlechtendahl in Linnaea **19**: 738 upon a Mexican plant I have not seen, but which from description may prove to be a typical *Metastelma;* in which case *Irmischia* will rank as a synonym of *Metastelma*.

As to types 2 and 3 mentioned above, I consider that these should be separated from *Melastelma* and made to constitute separate genera. [N. E. BROWN.]

Jacquemontia elongata Britton, sp. nov.

A slender vine, up to 5 m. long or longer, the branches and peduncles appressed-pubescent. Leaves ovate, membranous, slender-petioled, glabrous or nearly so, about 7 cm. long or shorter, the apex acute or acuminate, the base cordate, rounded or subtruncate; peduncles 5–10 cm. long, much longer than the petioles; inflorescence subcapitate, several-flowered; corolla blue to lavender, about 1.5 cm. in diameter.

Thickets, Trinidad, Tobago and northern Venezuela. Type from Manzanilla, Trinidad (*Britton 2191*). This plant has been referred to *J. pentantha* (Jacq.) Don.

Columnea tocoensis Britton, sp. nov.

Stems rather short, simple or little branched, clustered, 1.5 m. long or less; long, appressed, pubescent. Leaves oblong, 3–4 cm. long, appressed-pubescent, obtusish. Peduncles densely pubescent, 1.5 cm. long or shorter; calyx densely pubescent, about 8 mm. long, its lobes lanceolate, acutish; corolla yellow, about 4 cm. long, loosely villous with nearly white hairs, its slender tube about twice as long as the limb.

Pendent on forest trees, Trinidad. Type from Toco Road, near Valencia (*Britton, Hazen and Mendelson 1785*). This is, perhaps, the plant referred by Grisebach to *C. scandens*.

Columnea aripoensis Britton, sp. nov.

Branched, the branches rather stout, densely appressed-pubescent, 2 dm. long or longer. Leaves oblong, short-petioled 2.5–3.5 cm. long, finely appressed-pubescent, obtuse; peduncles densely villous, 8–12 mm. long; calyx 10–12 mm. long, appressed-pubescent, its lobes ovate, acute; corolla red, 3–4 cm. long, loosely pubescent with long jointed hairs, its tube gradually expanded above, about twice as long as the limb.

On trees, Heights of Aripo, Trinidad. (*Britton and Freeman 2340*, type).

Diapedium aripoense Britton, sp. nov.

Branching, strigillose, 1–1.5 m. high. Leaves elliptic-ovate, membranous, slender-petioled, rather strongly veined, long-acuminate at the apex, narrowed at the base, the lower about 2 dm. long, the upper much smaller; inflorescence several-flowered,

short-peduncled or nearly sessile; corolla red, villous, slightly curved, about 3 cm. long, its lobes about 6 mm. long.

Heights of Aripo, Trinidad. (Trinidad Herbarium *9860*, coll. *Broadway*, Jan. 10–26, 1922.)

Chimarrhis microcarpa Standley, sp. nov.

Branchlets stout, obtusely angulate, ochraceous, glabrous, the internodes 5–13 mm. long; stipules lance-oblong, attenuate, 3 cm. long, thin, brown, glabrous, caducous; leaves opposite, the petioles slender, glabrous, 2.5 cm. long; leaf blades elliptic, 11–19 cm. long, 5–8 cm. wide, acute, at base acute and decurrent upon the petiole, membranaceous, glabrous, the lateral nerves about 10 pairs, arcuate, laxly and irregularly anastomosing close to the margin; inflorescences axillary, cymose-paniculate, half as long as the leaves, 4–5 cm. long and broad, many-flowered, the peduncles slender, 3.5–5.5 cm. long, thinly puberulent, the pedicels 1–2 mm. long; capsules subglobose, 2 mm. long, obtuse at base, broadly rounded at apex, slender-costate, dark red-brown, glabrous, crowned by the low persistent calyx.

Type in the herbarium of the New York Botanical Garden, collected at Maraval, Trinidad, in 1904 (*I. Dannouse 6946*).

Because of the incompleteness of the available material, there is some doubt as to the proper reference of this plant to *Chimarrhis*, but it agrees well with that genus in the characters exhibited by the specimen studied.

76. AN UNDESCRIBED TREE OF PORTO RICO

Paralabatia portoricensis Britton & Wilson, sp. nov.

A tree 15 m. or more high, the twigs clothed with appressed ferruginous hairs. Leaves oblong-lanceolate, 6–11 cm. long, 2.5–4 cm. wide, acute or obtuse at the apex, rounded or somewhat acutish at the base; glabrous above except on the midvein, loosely pubescent beneath with rather long whitish hairs, the petioles about 1.5 cm. long; calyx-lobes 5, oblong-elliptic, 2 mm. long, pubescent on the back; corolla-lobes broadly elliptic to oval, 1.5 mm. long, unappendaged; staminodes filament-like; ovary 2-celled.

On limestone hills, northern Porto Rico. Type from Dominguito, near Arecibo (*H. T. Cowles 702*).

Related to *P. dictyoneura* (Griseb.) Pierre, of Cuba, but differing in the pubescence of the petioles and lower leaf-surfaces.

The Marsileas of the western United States

MARGARET STASON

Marsilea vestita Hooker and Greville is a widespread and variable species, occurring throughout the western and Pacific United States. It is subterrestrial or aquatic, occurring on the borders of marshy ponds which become dry as the season advances. Until 1902, when *Marsilea oligospora* Goodding was described, all material from this range was referred to *M. vestita*.

Marsilea vestita Hooker and Greville (Icones Filicum **2**: *pl. 159*. London, 1831) as described by Baker,[1] is a subterrestrial, tufted or widely creeping plant, with petioles 1–6 inches long, thinly clothed with appressed brown hairs, outer edges rounded and entire. The pedicels are short, erect, solitary, adnate to the upper part of the base of the conceptacle. The conceptacles are horizontal, persistently tomentose, unbordered, one-sixth to one-fifth inch long, with basal teeth prominent, and sori numbering about fifteen. The type locality of the species is the Columbia River region. The range of this species is given by W. R. Maxon in Abrams' Illustrated Flora of the Pacific States[2] as from British Columbia to southern California, east to South Dakota, Kansas, Oklahoma, and Texas.

Marsilea oligospora Goodding,[3] with Jackson Hole, Wyoming, as a type locality, is described as a plant 4–7 centimeters high, with leaflets woolly or becoming glabrous, 6–10 millimeters long, 3–7 millimeters wide, sporocarp solitary, 4–6 millimeters long, 4–5 millimeters wide, covered with long, straight and appressed, rarely somewhat woolly pubescence, rhaphe short, lower tooth short and blunt, upper tooth a mere rounded papilla or wanting, peduncle 5–8 millimeters long, sori 5–8 in each valve of the sporocarp, megaspores oval to rarely oblong, 6–9 in each sorus. The range of this species on the Pacific coast of North America as given by Maxon (loc. cit.) is Washington, Montana, Wyoming, and south in California to Tulare County.

[1] Baker, J. G. Handbook of the fern allies, p. 143. London, 1887.

[2] Abrams, Leroy. An illustrated flora of the Pacific States **1**: 34. Stanford Univ. Press, 1923.

[3] Goodding, L. N. Bot. Gaz. **33**: 66. 1902.

Here the statement is made that the number of sori to each valve of the sporocarp of *M. vestita* is 9–11, and the number of megasporangia to a sorus 12–20. This is in contrast to *M. oligospora*, described with sori 5–8 in each valve and megasporangia 6–9 per sorus.

On the basis of these distinctions as given by Maxon, an attempt was made to refer a collection of material from San Luis Obispo, California, made by Cecil Stockton, to one of these species. To examine the contents, the sporocarps were placed in boiling water after a small piece of the wall at one end had been cut away. Except when the sporocarp was immature, in the majority of cases the wall split almost immediately, the gelatinous ring bearing the sori emerged and the counting of the sori and megasporangia became a simple matter. From this San Luis Obispo collection, 106 sporocarps were examined. It was found that the upper tooth of the sporocarp ranged from short, though prominent, to long, sharp, and curved, the number of sori from 9 to 20 in each sporocarp, and the number of megasporangia in a sorus from 5 to 24.

A collection of material from Corning, California, made by Mrs. H. M. Hall in July, 1924, was examined in the same manner. In the twenty sporocarps examined, it was found that the upper tooth of the sporocarp varied from sharp and curved to blunt and rounded, in some cases there being a mere vestige of a tooth. Instances of this variation in the upper tooth were found in sporocarps on the same plant. Here the number of sori ranged from 15 to 20 and the megasporangia from 5 to 22, there being no evident correlation between the condition of the tooth and the number of the sori and megasporangia.

Collections of *Marsilea vestita* and *Marsilea oligospora* from several of the western herbaria and from the United States National Herbarium were next examined. For the privilege of studying this material, I am indebted to the kindness of Mr. W. R. Maxon for the loan of the United States National Herbarium collection of western Marsileas, to Professor Leroy Abrams of Stanford University for material from the Dudley Herbarium, to Professor P. A. Munz for material from the Pomona College Herbarium, to Professor Aven Nelson for a collection of *Marsilea oligospora* from the Rocky Mountain Herbarium, and to Professor N. L. Gardner for access to the

collection of the herbarium of the University of California. The data collected have been arranged in TABLE 1, in which the following symbols were used: *N* for the United States National Herbarium; *P* for the herbarium of Pomona College; *S* for the Stanford University Herbarium; *R* for the Rocky Mountain Herbarium; and *C* for the Herbarium of the University of California.

It may be seen from this table that in cases where the sporocarps bore a prominent or a sharp tooth, sori were found in numbers from 9 to 23 in each sporocarp, and megasporangia per sorus from 5 to 24. When the tooth of the sporocarp was reduced to a smooth, rounded protuberance the number of sori varied from 11 to 20 and the megasporangia from 1 to 18. It should be noted that in the examination of this material, often some megasporangia were broken from their sori and were lost before they could be counted, and also when the sori did not emerge from the sporocarp it was impossible to count the number of megasporangia. Such cases are left blank in the table.

In addition to the examination of the contents of the sporocarps, hand sections were made of their walls in the region of the tooth. This tooth was found to be a prolongation made up of stone cells, a continuation of the layers of such cells which form the outer wall of the sporocarp. The amount of this tissue varies with the size of the tooth and in cases where no tooth is present there are no extra stone cells developed.

Measurements of megasporangia of both types of sporocarps, those with a sharp tooth and those with none, revealed no differences in size and shape as suggested by Goodding, who observed the megaspores of *Marsilea oligospora* to be oval to barely oblong. There is some slight variation in the size and shape of the megaspores of a single sorus, but measurements of megaspores from several sporocarps of the same collection showed almost exactly the same range in size, length, and width in the two types. There also was no apparent difference in the size of the sporocarps in the two types. They vary in the sharp toothed form from 2 to 7 millimeters wide and from 3.5 to 10 millimeters long, and in the blunt toothed forms from 2.5 to 6 millimeters in width and from 4 to 8 millimeters in length.

The pubescence of the leaflets, petioles, and sporocarps was

found to vary widely in amount in the two types, that of the sporocarps of both being sometimes of appressed hairs and sometimes woolly-tomentose. There was no difference noted in the woolly pubescence occurring at the tufted bases of the plants.

A brief study of the distribution of the western forms of *Marsilea* brought out several interesting facts. *Marsilea oligospora* is attributed by Maxon to the Transition Zone of Merriam's classification,[4] while *Marsilea vestita* is definitely assigned to the Sonoran Zone. My study brought out rather clearly this same general limitation of distribution. It can be seen from the accompanying table, however, that several seemingly notable exceptions were found. In the case of the material from Corning, California, where sporocarps with conspicuous teeth and those with almost none were found, the habitat is definitely in the Sonoran Zone and in the Pacific semi-desert region, as indicated by the map of vegetation areas by Livingston and Shreve.[5] Another instance to be noted is the occurrence of both types of *Marsilea* along the Columbia River in the Great Basin type of vegetation area. This same mixture occurs in Lassen County, California, a district where the Great Basin and the Western Xerophyte forest vegetation areas intermingle. This region is of the Transition Zone. The sharp toothed form is not entirely confined to the Sonoran Zone or to Great Basin, Semi-Desert, or Grassland areas, but is found in the forest areas of western Montana and Colorado. It would seem therefore, that as far as the general vegetation areas are concerned, there is no sharp limitation in the distribution of either type.

Two specimens from central Florida (Eustis County, Florida, *George Nash 831*, and Orange Bend, Florida, *L. M. Underwood 337*, both in the United States National Herbarium and in the University of California Herbarium) are of the *Marsilea oligospora* type but decidedly extra-limital in distribution. Three sporocarps of the first collection and two of the second were examined. In none of these was there evidence of an

[4] Merriam, C. Hart. Life zones of the United States. U. S. Dept. Agr. Bull. 10. Washington, 1898.

[5] Livingston, B. E., and Shreve, F. Distribution of vegetation in the United States as related to climatic conditions. Carnegie Inst. Wash. Publ. 84. 1921.

TABLE I

State	Locality	Vegetation area	No. of sporocarps examined	2nd tooth of sporocarp sharp	2nd tooth of sporocarp blunt	No. of sori per sporocarp	No. of megasporangia per sorus	Herbarium
Washington	Columbia River opposite the Wenatchee	Great Basin	1		+	16		N
	Sauvies Island	" "	1	+		18	7–10	N
	Falcon Valley	" "	2		+	17–18	4–11	N
	Sentinel Bluffs	" "	1	+		17		N
	Pullman	" "	1	+		18	9–12	S
	Klichitat Co. along Columbia	" "	2	+		13–14	9–10	S
	Lake Chelan	Grassland	2	+		15–17	9–9	N
Oregon	The Dalles	Great Basin	1	+		18		N
	" "	" "	1	+		17	9–8	N
	" "	" "	1	+		12	8–10	N
	Klamath Falls	" "	1	+		16	6–8	N
	Columbia River	" "	1	+		19	12–13	N
California	Pine Creek	" "	1		+	16	8	C
	Eagle Lake	" "	1		+	11	Undeveloped	C
	Honey Lake	" "	1	+		20	"	C
	Lake Tahoe	Western Xerophyte forest	1		+	16	7–10	N
	Corning	Pacific semi-desert	20	+	+	17–20	6–22	C
	Yolo County	" "	1	+		20	8–12	P
	Dos Palos	" "	1	+		17	7–10	N
	San Luis Obispo	" "	1	+		14	10–12	N
	" " "	" "	106	+		9–20	5–24	C
	Tulare County	" "	1	+		16	14–12	P
	Tulare	" "	2	+		17–18	10–12	P
							9–13	C
	Chico	" "	1	+		18	12	S
	Galt	" "	1	+		23	6	C
	Emigrant Gap	" "	1	+		20		C
	Ramona	" "	1	+		22	8–9	P
	Laguna	" "	2	+		19–16	10–16	P
							5–9	
	Kenworthy	" "	1	+		16		P
	Cuyamaca Lake	" "	2	+		18–20	10–12	P-C
	West Riverside	" "	1	+		18	9	C
Montana	Blackfoot River	W. X. forest	1		+	15	7–5	N
	N. W. Montana	" " "	1	+		16	10–11	N
Idaho	Weiser	Great Basin	1	+		19		P
Nevada	Winnemucca	" "	1	+		16	8–9	N
Wyoming	Jackson Hole	W. X. forest	1		+	15	1–1	N
	Kendall	" "	2		+	15	9–6	
	Sublette County	" "	1		+	14	6–11	R
Colorado	Sagnache	" "	1	+		15	8–5	N
	Boulder	" "	1	+		20	10–12	P
N. Dakota	Benson County	Grassland	1	+		16		P
S. Dakota	Woolsey	"	1	+		16		N
Texas	Dallas	"	2	+		20–19	6–12	N-P
Florida	Eustis Co	S. E. Evergreen forest	3		+	13–18–20	Undeveloped	N-C
	Orange Bend	S. E. Evergreen forest	2		+	15–17	none	C-N

upper tooth. The number of sori varied from 13 to 20. An interesting feature of these sporocarps was the seeming absence of megaspores. In the Eustis County collection the sporocarps were evidently immature, as shown by the condition of the microsporangia, and in developing sori the microsporangia can be distinguished before the megasporangia are sufficiently developed for recognition. This collection therefore is not conclusive. In the Orange Bend material, however, the microsporangia were well developed and the microspores numerous, but there was no evidence of megasporangia. This is a condition not met with elsewhere in the study of the western material where the sporocarps had reached maturity.

It seems evident that there is no clear cut distinction between the two forms of *Marsilea* that might be spoken of as the *vestita* and the *oligospora* types, in habitat, distribution, form of the plant, pubescence, the number of sori in a sporocarp, the number of megasporangia in a sorus, and no correlation between these factors and the most pronounced variation, that of the tooth of the sporocarp. Even in the character of the tooth, there seems no definite line between forms with the second tooth present and those without, there being all gradations between them. Possibly there may be here in *Marsilea vestita* what Turesson[6] calls an 'Ecospecies,' that is, a widely distributed and variable species in which ecological factors have caused differentiation into two hereditary types. The *oligospora* type may then be termed an 'Ecotype,' and it may be supposed to be a subtype of the Ecospecies which has arisen by response to some possible habitat factors. Such an hypothesis can only be tested by culture methods, and only vaguely suggested by the examination even of more ample herbarium material than was placed at my disposal.

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[6] Turesson, Gote. The scope and import of genecology. Hereditas 4: 171–176. 1923.

Pollen grain morphology in the classification of the Anthemideae

R. P. Wodehouse

(with two text figures)

The spiny character of the pollen grain of the Carduales has long been a matter of comment. It is almost as universal among the Carduales as the more salient characters of the order, such as, for example, the aggregation of the flowers on a receptacle surrounded by an involucre, the union of the anthers into a tube, or the reduction of the calyx to bristles or scales, or its entire absence. This spiny character of the pollen grain of the Carduales can be made to serve admirably in their classification, because the arrangement, shape, and size of the spines varies more or less continuously throughout the order just as do the grosser morphological characters. From an examination of the pollen grains alone it is always possible to tell to which of the three families of the Carduales a species belongs, and nearly always even the tribe. In spite of this, however, pollen grain morphology is rarely used in taxonomic work.

That this spiny character of the pollen grain arose independantly in the Carduales seems probable from its absence in such related families as Lobeliaceae and Calyceraceae. In the Campanulaceae and Dipsacaceae, though minute spines are present, they do not resemble the spines of the Carduales and appear to bear no relation to them. Moreover in the Carduales, this spiny character reaches its best development in the more generalized forms of the Carduaceae, as, for example the Heliantheae, Astereae, and Vernoneae. Needless to say spinyness has arisen independently in many other families, notable among which are the Convolvulaceae and Malvaceae, but in none of these do the spines themselves or their arrangement resemble those of the Carduaceae at all closely. The spines of the Carduaceae may be described as sharp pointed cones which are a part of the exine, not merely articulated or attached to it, and they are partly or entirely covered by the perinium or outer layer of material which overlies the exine. The number, arrangement and size of the spines varies considerably in the

different species of the Carduaceae, but they are nearly always geometrically arranged and large enough to constitute the most conspicuous character of the grain. There is only one character of the grain which is more constant for the family, and that is the three germinal apertures situated in the three longitudinal folds which accomodate the changes in volume resulting from the changes in moisture content. This character, however, is not confined to the Carduales.

The Ambrosiaceae are regarded as an offshoot from the Carduaceae. That they may be regarded as more highly developed than the latter is evidenced by the simplification of the floral parts, the extreme reduction or total loss of calyx and corolla, and the extreme reduction of the involucre of the pistillate heads and the accrescence of its bracts to form a pod enclosing the achenes in the genera *Hymenoclea*, *Ambrosia*, *Franseria*, and *Xanthium*. Associated with this simplification of floral parts is a reduction in spinyness of the pollen grains. The amount of this reduction varies somewhat in the different genera. In *Iva* the spines are low and rounded on the top but still prominent. In *Franseria* and *Ambrosia* they are similar but somewhat less prominent, while in *Xanthium* they are reduced to mere specks, and in some species of this genus are scarcely visible.

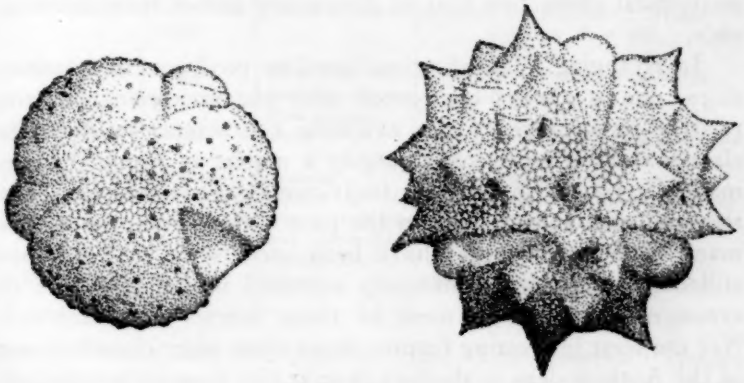
This reduction of spinyness is entirely in keeping with the anemophilous habit of this family, and probably, therefore, can be regarded as an ecological response to this mode of pollination, as is the case with the reduction of floral parts and the adoption of the dioecious or monoecious habit by most of the species.

On the other hand, the Cichoriaceae, which are probably less related to the Carduaceae than are the Ambrosiaceae, possess the characteristic spines of the Carduaceae, though nearly all the other characters of the grains are quite different. Nevertheless the resemblance of the spines of the Cichoriaceae to those of the Carduaceae is suggestive of a common origin.

In spite of the fundamental quality of the spiny character among the Carduales, in three separate tribes of the Carduaceae spinelessness has been independently developed. These three tribes are the Mutisieae, Cynareae and Anthemideae. The Mutisieae are all spineless, and as far as these studies have gone, no trace of spines has been found. This entire absence of

spines throughout the whole tribe suggests that the group arose from a spineless mutant from the Carduaceae stock.

In the tribe Cynareae the genus *Centaurea* comprises species exhibiting all degrees of spinyness, from its well developed form characteristic of the tribe to its entire absence. This condition suggests that the Centaureas are in the process of developing spinelessness.



1 2

FIG. 1. Pollen grain of *Crossostephium artemisioides* Less. (*Tanacetum chinensis* Gray, *Artemisia chinensis* Vahl., not L.) 20.9 μ diam. This form of pollen grain is characteristic of the genus *Crossostephium* and the allied genera *Sphaeremeria*, *Vesicarpa*, *Chamartemisia*, *Picrothamnus*, *Artemisia* and *Artemisiastrum*, according to the classification of Rydberg (1916), but is not found elsewhere in the Anthemideae.

FIG. 2. Pollen grain of *Tanacetum camphoratum* Less. 29.7 μ in diameter. This form of pollen grain is characteristic of all species of the genus *Tanacetum*, and is similar to that of all species of the tribe Anthemideae, except those of the genera mentioned above.

In the Anthemideae the character of spinelessness is of the greatest interest, for it appears abruptly and with little suggestion of transition, and is confined to a group of plants of close but disputed relationships, comprising the following seven genera, according to the classification of Rydberg[1]: *Sphaeromeria*, Nutt., *Vesicarpa*, Rydb., *Chamartemisia*, Rydb., *Crossostephium*, Less., *Picrothamnus*, Nutt., *Artemisia* L., *Artemisiastrum* Rydb. (FIG. 1).

The common character of spinelessness of these seven genera

[1] Rydberg, P. A. North American Flora **34**: 217. 1916.

would indicate that they had all originated from a common ancestor, a spineless mutant from the Anthemideae stock, or else spinelessness arose independently at two or more points. That the former is more likely seems cogent from the following facts. The pollen grains of these seven genera are almost indistinguishable from each other and show as little variation in size as would be expected within a single genus. Moreover the grosser anatomical characters hint at divergence rather than convergence.

In arranging a classification based on phylogenetic relationships, one is always confronted with the uncertainty of the relative importance of the available characters, so that the classification often becomes largely a matter of personal judgment, varying with different individuals. That this has been the case with these plants in the past is fully manifest by the many classifications that have been used, some of which are still extant, and is permanently recorded in the long lists of synonyms with which most of these species are burdened. Not the least interesting feature about these older classifications of the Anthemideae is the fact that at one time or another, all of the seven genera, except *Sphaeromeria* and *Chamartemisia*, have been regarded as belonging to the genus *Artemisia*, and yet this has been done entirely without reference to pollen grains, which goes to show that there are recognizable anatomical characters which may be interpreted to mean that there is a close relationship between these seven genera. On the other hand, the first three of these genera have more frequently been regarded as belonging to *Tanacetum*.

The difficulty of establishing adequate grounds for separating these genera from each other and from *Tanacetum* becomes apparent from TABLE I, which is taken from Hall and Clements.[2] Here the authors have selected and tabulated in a convenient form, all the significant characters that have been used in the classification or segregation of this group.

In this treatment Hall and Clements state that they prefer to regard the first four genera listed in TABLE I as *Tanacetum*, and the last three as *Artemisia*. The fifth (*Crossestephium*), according to Rydberg, comprises four species, three of which

[2] Hall, H. M., & Clements, F. E. The phylogenetic method in taxonomy. Carnegie Inst. Washington Publ. 326. 1923.

TABLE I

	Anther-tips	*Inflorescence*	*Pappus*	*Corolla of marginal flowers*	*Receptacle*
TANACETUM	Ovate, obtuse	Cymose or solitary by reduction	Coroniform	Oblique, somewhat ligulate	Naked
VESICARPA	Ovate-lanceolate	Cymose	Wanting	Nearly tubular	Pubescent
SPHAEROMERIA	Ovate, "obtusish"	Cymose or solitary	Wanting	Nearly tubular, slightly if at all oblique	Naked
CHAMARTEMISIA	Subulate	Solitary or two, probably reduced from a cyme	Coroniform	Nearly tubular; no ligules	Naked
CROSSOSTEPHIUM	Subulate	Panicle	Coroniform	Nearly tubular; no ligules; in 2 rows	Essentially naked
PICROTHAMNUS	Subulate	Racemose	Wanting	Short, 2-cleft	Naked
ARTEMISIA	Lanceolate or subulate	Panicled or the panicle reduced and raceme-like or spike-like	Wanting	Tubular, often oblique	Naked or pubescent
ARTEMISIASTRUM	Subulate	Panicled	Wanting	Tubular	Chaffy

are American and one Asiatic. The three American species Hall and Clements prefer to place in *Artemisia*, but the single exotic species they allow to remain, making *Crossostephium* a monotypic genus.

Hall and Clements contend that Rydberg accords generic rank to segregates which are of only specific, or at best, subgeneric value. They state that the eight genera employed by Rydberg really constitute only three, *Tanacetum*, *Crossostephium* (of a single species) and *Artemisia*. Whether Rydberg's genera are too numerous or too few is a matter of little consequence at the present time, for the "question of generic limits is one of criteria" and largely a matter of opinion, and can only be answered when the answer to the question What is a genus? has been agreed upon. Nevertheless the groupings as pointed out by Rydberg are there, and should be recognized in some way. What is a matter of much greater importance is the interrelationship between the groups, for, as Hall and Clements have so frequently emphasized, it is the business of classification to suggest relationships. In this case, however, as we shall see, the evidences of relationship are conflicting, and throw some doubt on the arrangement.

An analysis of the table reproduced above shows that, re-

gardless of pollen characters, there is as much similarity between *Artemisia* and the three genera *Vesicarpa*, *Sphaeromeria*, and *Chamartemisia*, as there is between these three genera and *Tanacetum*. For example, if we compare *Vesicarpa* with *Tanacetum* and with *Artemisia*, using the characters in TABLE I, the anther tips which are ovate-lanceolate, are intermediate. The 'inflorescence' is cymose, thus resembling *Tanacetum*. The pappus is absent, thus resembling *Artemisia*, for in all true species of *Tanacetum* it is said to be present and coroniform. The corolla of the marginal flowers is nearly tubular, thus resembling *Artemisia*, in which they are tubular and sometimes oblique, more closely than it does *Tanacetum*, in which they are oblique and somewhat ligulate. The receptacle is pubescent, thus resembling *Artemisia* more closely than *Tanacetum*, for the latter may be naked or pubescent, while the former is always pubescent. Thus of the five characters most generally used, we have only that of the cymose 'inflorescence,' pointing towards *Tanacetum*. Of the other characters one (viz. the absence of pappus) points definitely towards *Artemisia*. The remaining three are intermediate, but two of them (viz. the tubular corollas of the marginal flowers and the pubescent receptacle) point more strongly towards *Artemisia*. Similarly if we compare *Sphaeromeria* and *Chamartemisia* with *Tanacetum* and *Artemisia*, we find that the evidence of relationship is about equally divided between them, so that, at best, the relationship revealed by the gross anatomical characters is vague and uncertain.

In contrast to this, the spineless character of the pollen grain is perfectly constant. All those of the genera *Vesicarpa*, *Sphaeromeria* and *Chamartemisia* are spineless and none of these species shows any indication of ever having had spines (FIG. 1). In this and their other characters they are nearly indistinguishable from the Artemisias. On the other hand they resemble *Tanacetum* only in the possession of the general characters common to the *Anthemideae*. Therefore they do not appear to belong to the genus *Tanacetum* (FIG. 2).

The spinelessness of the pollen grains of these three genera is evidence that they are more closely associated with *Artemisia*, as are also the other spineless grained Anthemideae (*Crossostephium*, *Picrothamnus* and *Artemisiastrum*), than they are with *Tanacetum*, but it does not necessarily follow that the

whole seven should be considered as a single genus, for there are obviously other characters that serve to separate them from each other; but if one does not choose to recognize these characters as of generic value, then it would be necessary to join all of these genera with *Artemisia*. However, observations in other families show that the pollen characters are more often family characters than generic.

These studies of the pollen grain morphology of the Anthemideae show that the genera *Sphaeromeria*, *Vesicarpa*, *Chamartemisia*, *Crossostephium*, *Picrothamnus*, *Artemisia* and *Artemisiastrum* are all spineless, and consequently probably derived from a common spineless ancestor, because all the other members of the Anthemideae, including *Tanacetum*, are conspicuously spined. Since it is the business of taxonomy not merely to catalogue species, but more especially to show relationships and suggest the probable trend of evolution, the anatomy of the pollen grain is fully as deserving of attention as are any of the more generally used grosser anatomical characters.

INDEX TO AMERICAN BOTANICAL LITERATURE
1925–1926

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